Functional and Anatomical Correlates of Language Expertise

Thesis

presented to the Faculty of Arts

of

the University of Zurich

for the Degree of Doctor of Philosophy

by

Stefan Elmer

of Elm GL, Switzerland

Accepted in the spring semester 2010

on the recommendation of

Prof. Dr. Lutz Jäncke

Prof. Dr. Martin Meyer

Zurich, 2012

ACKNOWLEDGEMENTS

Even though there are many people I wish to thank for having supported me during the entire Ph.D. period, in the following paragraphs only few of them are gratefully acknowledged. First of all, I would like to thank my supervisors, Prof. Dr. rer. nat. Lutz Jäncke, and Prof. Dr. rer. nat. Martin Meyer who supported me since my early years as a student at the division of Neuropsychology at the University of Zurich. In particular, I am grateful to Prof. Lutz Jäncke and Prof. Martin Meyer for their support and especially for giving me the opportunity to unfold an exhaustive topical freedom.

Furthermore, I would like to thank all co-workers and colleagues of the division of Neuropsychology at the University of Zurich for creating a pleasant working environment and for the fruitful scientific stimulation. A special thank goes to the doctors Tino Zaehle, Mathias Oechslin, Jürgen Hänggi, Pascale Sandmann, Michael Brügger, Andreas Pedroni, Kai Lutz as well as to the Ph.D. students Franz Liem, Martina Hurschler, Jürg Kühnis, Philip Reich, Katharina Rufener, and Cyrill Ott. I am especially grateful to my friend and office colleague, Dr. Monika Kast for the warm and stimulating working atmosphere during my entire Ph.D. period.

Finally, my deepest thanks go to my family and to my friends. I am particularly indebted to my parents and to my brother for their ongoing support and encouragement. My warmest thank goes to Maria Gonzalez for her love and support during my Ph.D. period.

CONTENTS

I. SUMMARY

A number of previous studies have shown that intensive training and expertise in a particular domain are associated with functional and structural changes of the human brain. Exactly these altered brain characteristics as a function of intensive training have previously well been documented in cross-sectional (Bangert & Schlaug, 2006; Baumann, Meyer, & Jancke, 2008; Elmer, Meyer, & Jäncke, 2011; Pantev, Roberts, Schulz, Engelien, & Ross, 2001) and longitudinal (Bangert & Altenmuller, 2003; Bezzola, Merillat, Gaser, & Jancke, 2011; Draganski et al., 2004; Hyde et al., 2009) studies by using different methodologies. In this context, an abundance of work dedicated to investigate the influence of intensive training in professional musicians, found convergent evidence for an altered brain architecture, most notably in auditory (Jancke, 2009; Munte, Altenmuller, & Jancke, 2002; Schlaug, Jancke, Huang, & Steinmetz, 1995), somatosensory, and motor brain regions (Amunts et al., 1997; Bangert et al., 2006; Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995). Furthermore, previous work performed with musicians not only showed that brain functions and structures can change as a function of training, but notably also that these architectural changes can indeed favour cognitive and perceptual abilities in domains which were not explicitly trained (Aleman, Nieuwenstein, Bocker, & de Haan, 2000; Bilhartz, Bruhn, & Olson, 1999; Brochard, Dufour, & Despres, 2004; Gromko & Poorman, 1998; Magne, Schon, & Besson, 2006; Marie, Magne, & Besson, 2011; Schlaug, Norton, Overy, & Winner, 2005).

Basing on this previous evidence for neuroplasticity and transfer effects in professional musicians, the present work was dedicated to systematically address functional and structural neuronal reorganization in language experts. In particular,

the present work aimed at uncovering the effect of intensive language training as experience by simultaneous interpreters (SIs) on 1) lexical processing within and across the languages intensively trained, 2) on structural white matter adaptations in regions supporting articulation, sensory-to-motor coupling mechanisms, and cognition, and 3) on functional and behavioural transfer effects originating from language training. With these purposes in mind, and by adopting cross-sectional designs, I postulated that neuronal reorganisation and transfer effects may originate as a consequence of the processing demands necessary for translating a source language into a target language.

The aim of **study A** (EEG), entitled "*Simultaneous Interpreters as a Model for Neuronal Adaptation in the Domain of Language Processing"*, was to examine the impact of language training as experienced by SIs on lexical processing within and across the native (L1) and non-native (L2) languages. With this purpose in mind, eleven native German SIs and controls matched in L2 proficiency and age of acquisition were asked to judge whether auditory presented disyllabic noun pairs were either semantically congruent or incongruent. In terms of electrophysiological responses, we observed an earlier negative deflection of the N400 component in the SIs group, in comparison to the controls, while detecting incongruent trials within the native (L1) and non-native (L2) languages, as well as during the incongruent German-English condition (GE). These earlier negative responses were interpreted as indicating a training-related altered sensitivity to lexical processing within L1 and L2 as a function of language expertise. Otherwise, the tonic increased N400 responses we observed in the SIs while processing semantic congruent noun pairs which were presented in the opposite direction as usually trained (i.e., from L1 to L2)

were interpreted as reflecting the engagement of additional cognitive resources necessary for accomplishing an untrained and therefore unusual language task.

In **study B** (DTI), entitled "*Differential Language Expertise Related to White Matter Architecture in Regions Subserving Sensory-Motor Coupling, Articulation and Interhemispheric Transfer*", we investigated white matter alterations as a function of long-term language training. Basing on the assumption that simultaneous interpreting places high demands on articulation and sound-to-motor mapping mechanisms, as well as on cognitive functions which are vital for executing fast interpretations, we expected to provide evidence for an altered white matter architecture in brain regions involved in the motor control of speech and cognition. In line with our hypothesis, we found evidence for an altered white matter architecture in the SIs group, in comparison to the controls, in the left anterior insula and in the head of the right caudate nucleus, both structures previously shown to be involved in supporting articulation and sensory-to-motor coupling mechanisms. Furthermore, we revealed a differential white matter architecture in the SIs group in the most anterior part of the corpus callosum, a structure being composed of fibre bundles connecting the two frontal lobes. These training-related white matter adaptations we revealed in the anterior part of the corpus callosum are supposed to optimise the interplay between the two frontal lobes which are strongly involved in controlling executive functions during interpreting.

In **study C** (fMRI), entitled "*Intensive Language Training and Attention Modulate the Involvement of Fronto-Parietal Regions During a Non-Verbal Auditory Discrimination Task"*, we investigated behavioural and functional transfer effects originating from language training. In particular, we explored whether the intensively trained attention functions of SIs may facilitate the discrimination of non-verbal stimulus attributes. With this purpose in mind, we used the fMRI technique and compared brain activation maps in SIs and control subjects while the subjects performed a non-verbal pitch discrimination task which strongly relies on auditory attention and categorization functions. Whereas the two groups did not differ in terms of correct responses, results showed an expertise-related modulation of fronto-parietal brain regions while performing the task. This expertise-related modulation was manifested by increased brain responses in the left angular gyrus in conjunction with reduced brain activity in the right frontal operculum. The anterior to posterior displacement of brain responses we observed in the SIs group was interpreted as being particularly advantageous for relieving the functional capacity of the frontal lobe, which is indeed strongly involved in supporting executive functions during interpreting, from additional cognitive loads.

II. ZUSAMMENFASSUNG

Zahlreiche neurowissenschaftliche Untersuchungen haben gezeigt, dass das menschliche Gehirn die Eigenschaft besitzt sich durch Umwelteinflüsse und Training funktionell und strukturell zu verändern. Diese trainingsbedingte Modulationen von Hirnfunktionen und Hirnstrukturen wurden sowohl anhand von Längsschnitts- (Bangert et al., 2003; Bezzola et al., 2011; Draganski et al., 2004; Hyde et al., 2009) und Querschnittstudien (Bangert et al., 2006; Baumann et al., 2008; Pantev et al., 2001), wie auch durch die Verwendung unterschiedlicher Messtechniken wiederholt belegt. In diesem Zusammenhang sind insbesondere Studien zu erwähnen, die trainingsbedingte Reorganisationsprozesse in perisylvischen, somatosensorischen, und motorischen Hirngebieten von professionellen Musikern beschrieben haben (Amunts et al., 1997; Bangert et al., 2006; Elbert et al., 1995; Jancke, 2009; Munte et al., 2002; Schlaug et al., 1995). Neuere Arbeiten haben sogar gezeigt, dass diese trainingsbedingten funktionellen und strukturellen Veränderungen sensorische und kognitive Prozesse begünstigen können, die nicht explizit trainiert wurden (Aleman et al., 2000; Bilhartz et al., 1999; Brochard et al., 2004; Gromko et al., 1998; Magne et al., 2006; Marie et al., 2011; Schlaug et al., 2005).

Basierend auf den Befunden, die aus der Erforschung von professionellen Musikern hervorgehen, befasste ich mich in dieser Dissertationsarbeit mit der Fragestellung, wie intensives Sprachtraining und Sprachexpertise die Funktionen und Strukturen des menschlichen Gehirnes verändern können. Aufgrund des intensiven Trainings und der Beanspruchung von kognitiven, sensorischen, und sprachmotorischen Funktionen können bei Simultandolmetschern ähnliche trainingsbedingte

Veränderungen von Hirnstrukturen und Funktionen erwartet werden, wie sie anhand von professionellen Musikern aufgezeigt wurden. Die vorliegende Dissertationsarbeit beinhaltet drei Querschnittstudien zur Erforschung von Plastizität und Transfer-Effekten bei Simultandolmetschern. Ziel dieser drei Studien war es, die folgenden Fragestellungen zu beantworten: 1) Welchen Einfluss haben Sprachtraining und Expertise auf die lexikalische Verarbeitung von Einzelwörtern? 2) Begünstigt intensives Sprachtraining Veränderungen der weissen Substanz in Hirngebieten, die an Sprachmotorik und Kognition beteiligt sind? 3) Können Simultandolmetscher die intensiv-trainierten Aufmerksamkeitsfunktionen einsetzen, um nicht-verbale Reize effizienter zu verarbeiten?

Studie A (EEG) mit dem Titel "*Simultaneous Interpreters as a Model for Neuronal Adaptation in the Domain of Language Processing"* hatte zum Ziel, den Einfluss von Sprachtraining auf die lexikalische Verarbeitung von Einzelwörtern zu untersuchen. Mit diesem Ziel im Auge untersuchten wir professionelle Simultandolmetscher und eine Kontrollgruppe während dessen die Probanden eine lexikalische Entscheidungsaufgabe lösten die darin bestand, zweisilbige Wortpaare innerhalb der Muttersprache, innerhalb der Fremdsprache, wie auch zwischen den beiden Sprachen auf semantische Kongruenz zu überprüfen. Die elektrophysiologischen Daten zeigten eine frühere und ausgeprägtere Negativierung der N400 Komponente bei den Simultandolmetschern im Vergleich zur Kontrollgruppe, während dessen die Probanden inkongruente Wortpaare innerhalb der Muttersprache (L1) und der Fremdsprache (L2) verarbeiteten. Vergleichbare Effekte wurden auch während der inkongruenten Deutsch-Englisch Bedingung beobachtet. Diese frühere Negativierung der N400 Komponente deuteten auf eine veränderte Sensitivität der lexikalisch-

semantischen Verarbeitung als Funktion der Sprachexpertise hin. Weiterhin wurde festgestellt, dass Simultandolmetscher bei der Verarbeitung von kongruenten Wortpaaren, die in der entgegengesetzten Sprachrichtung als normalerweise trainiert präsentiert wurden (von L1 zu L2), tonisch erhöhte N400 Amplituden zeigten. Dieses Ergebnis deutet darauf hin, dass Simultandolmetscher bei dieser untrainierten und deswegen ungewohnten Aufgabe mehr kognitive Ressourcen als Kontrollprobanden benötigen, um die Aufgabe zu lösen.

In **Studie B** (DTI) mit dem Titel "*Differential Language Expertise Related to White Matter Architecture in Regions Subserving Sensory-Motor Coupling, Articulation and Interhemispheric Transfer"*, untersuchten wir trainingsinduzierte Veränderungen der weissen Substanz im Zusammenhang mit Sprachexpertise. Ausgehend von der Hypothese, dass Simultandolmetschen kognitive und sprachmotorische Funktionen erheblich beansprucht, erwarteten wir trainingsbedingte Veränderungen der weissen Substanz in Hirnregionen, die Sprachmotorik und kognitive Prozesse steuern, zu beobachten. Unsere Ergebnisse unterstützen diese Arbeitshypothese indem Simultandolmetscher anatomische Veränderungen in der linken vorderen Insel und im rechten Kopf des nucleus caudatus zeigten, beides Hirnregionen, die massgebend an der Steuerung der Sprachmotorik beteiligt sind. Weiterhin zeigten die Simultandolmetscher eine veränderte Architektur der weissen Substanz im vorderen Anteil des corpus callosum, einem Faserbündel, das beide Frontallappen miteinander verbindet. Diese morphologische Veränderung ermöglicht wahrscheinlich ein optimales Zusammenspiel zwischen frontalen Hirnregionen, die auf fundamentale Weise an der Steuerung und an der Kontrolle von kognitiven Prozessen beteiligt sind.

In **Studie C** (fMRI) mit dem Titel "*Intensive Language Training and Attention Modulate the Involvement of Fronto-Parietal Regions During a Non-Verbal Auditory Discrimination Task"*, untersuchten wir den Einfluss von Sprachtraining und Expertise auf die Diskriminierung von nicht-verbalem Stimulus Material. Diese Studie basiert auf der Hypothese, dass die intensiv trainierten Aufmerksamkeitsfunktionen bei Simultandolmetschern ebenfalls eingesetzt werden können um nicht-verbale Reize effizienter zu detektieren. Im Rahmen einer Diskriminationsaufgabe, die darin bestand die Aufmerksamkeit auf einen bestimmten Zielreiz zu lenken und diesen per Knopfdruck zu erkennen, wurden folgende Ergebnisse beobachtet: obwohl sich Simultandolmetscher und Kontrollprobanden in der Verhaltensleistung nicht unterschieden, zeigten die Sprachexperten unterschiedliche Aktivierungsmuster in frontalen und parietalen Hirngebieten. Insbesondere die beobachtete Verlagerung der Hirnaktivität von frontalen zu parietalen Hirnregionen dient wahrscheinlich dazu das Stirnhirn, welches beim Simultandolmetschen zur Ausübung der kognitiven Kontrolle erheblich beansprucht wird, zu entlasten.

1. INTRODUCTION

1.1. Plasticity and Neuronal Reorganisation

Several decades ago there it was supposed that whereas sensory- and motor-related cortical and subcortical brain structures are unalterable after ontogenesis, memory-related brain regions like the hippocampus are functional and structural more susceptible to neuronal reorganization processes (Jancke, 2009). However, in the last years umpteen studies conducted with different methodologies could show that the human brain changes its structure and function throughout the entire lifespan (Gogtay et al., 2004; Jancke, 2009; Parbery-Clark, Strait, Anderson, Hittner, & Kraus, 2011) and that almost all brain areas are malleable in conjunction with training and expertise (Jancke, 2009; Kraus & Chandrasekaran, 2010; Maguire et al., 2000). These functional and structural adaptations as a consequence of environmental influences or intensive training are called plastic reorganisations, or simply neuroplasticity. To date, a plethora of studies have highlighted different organisation principles of plasticity at the molecular, cellular, physiological or micro- and macro-anatomical level.

A milestone in the concept of plasticity was done in 1949 by the Canadian neuropsychologist D.O. Hebb who firstly proposed the "Hebbian theory of learning" (Hebb.D.O., 1949). This theory bases on the assumption that synapses strengthen with the use and that neurons that fire together wire together. In this context, D.O. Hebb postulated the following principle of plasticity: “When an axon of cell A is near enough to excite cell B and repeatedly or persistently takes part in firing it, some growth process or metabolic change take places in one or both cells such that A’s

efficiency, as one of the cells firing B, is increased" (Hebb.D.O., 1949). Several years later, Hebb's law was widened by the discovery of the cellular mechanism of long-term potentiation (LTP) (Bliss & Lomo, 1973; Douglas, 2011; Lomo, 1966; Lomo, 2003). This learning mechanism at the cellular and molecular level was originally associated with an increased synaptic strength in the perforant pathway of the dentate gyrus of the hippocampus, and was first discovered in animal models by stimulating pre-synaptic fibres with high-frequency electrical pulses (Bliss et al., 1973; Douglas, 2011; Lomo, 1966; Lomo, 2003). Otherwise, when in the same model electrical pulses are presented at a low frequency; long-term depression (LTD) can be induced (Ewert, 1998; Malenka & Bear, 2004). At a molecular level, LTP and LTD were shown to depend on the properties of the N-methyl-D-aspartate receptor, its agonist glutamate, as well as on the functional properties of Calcium and magnesium ions (Ewert, 1998). A further implication of LTP / LTD at the cellular level was elucidated several years later by Tashiro and Yuste (Tashiro & Yuste, 2003; Tashiro & Yuste, 2004) which could show, by adopting biological nanotechnology methods, that during LTP / LTD, dendritic spines appear and disappear on a dendrite in the latency range of seconds. This can lead to an increased or reduced surface area which is available on the dendrites for building contacts with axon terminals. This short-term plastic phenomenon was shown to be driven by calcium influx in the dendritic receptors and to be related to mRNA / DNA cascades of molecular processes (Tashiro et al., 2003; Tashiro et al., 2004).

An alternative approach for studying brain plasticity at the behavioural level was described for example by Ramachandran (Ramachandran, Rogersramachandran, & Stewart, 1992) by investigating patients suffering from phantom-limb pain, a

phenomenology common in people who have undergone the amputation of a limb or even parts of them. In a series of elegant studies, (Ramachandran, Rogersramachandran, & Cobb, 1995; Ramachandran & Rogers-Ramachandran, 2000), Ramachandran could show that the cortical structures that code the sensory perception of the amputated limb are incorporated into the somatotopic representation of the body parts that are represented nearby the amputated limb. At the end of the 1980s, the emergence of the magnetic resonance imaging (MRI) technique opened the possibility for functional and structural in vivo human brain mapping. The MRI technique is particularly fruitful in that it permits to perform correlative measurements of brain activity by measuring blood oxygen saturation (BOLD), to perform morphometric analyses (gray and white matter density, volume, cortical thickness, and surface area), or to identify and measure white matter fibre tracts basing on the principle of water molecules diffusion (DTI). Together with the method of electroencephalography (EEG) in which electrical brain activity can be measured directly on the scalp in the form of voltage fluctuations, the fMRI, MRI, and DTI techniques permit to uncover functional and structural neuroplastic changes of the brain. To date such architectural changes have not only been demonstrated in healthy adults as a consequence of intensive training or environmental influences (Draganski et al., 2004; Jancke, 2009; Maguire et al., 2000; Munte et al., 2002), but also in children (Magne et al., 2006; Meyer et al., 2011) and in elderly subjects (Heuninckx, Wenderoth, & Swinnen, 2008; Lustig, Shah, Seidler, & Reuter-Lorenz, 2009).

In the last twenty years, the impact of intensive training on the functional and anatomical architecture of the human brain has been well documented for example by investigating professional musicians with a variety of brain imaging and electrophysiological techniques (Jancke, Shah, & Peters, 2000; Schlaug et al., 1995; Schneider, Sluming, Roberts, Bleeck, & Rupp, 2005). Notably, the impact of musical training on cortical reorganization processes was not only shown in professional musicians (Munte et al., 2002), but also in laymen undergoing a short period of musical training (Moreno et al., 2009), and in children (Bilhartz et al., 1999; Hyde et al., 2009; Kraus et al., 2010; Meyer et al., 2011). In the context of musicianship, umpteen studies provided evidence for an altered grey (Abdul-Kareem, Stancak, Parkes, & Sluming, 2011; Bermudez, Lerch, Evans, & Zatorre, 2009; Schlaug et al., 1995) and white (Bengtsson et al., 2005; Imfeld, Oechslin, Meyer, Loenneker, & Jancke, 2009; Schmithorst & Wilke, 2002) matter architecture, most notably in auditory-related, somatosensory, and motor brain regions. For example, Schlaug and colleagues (Schlaug et al., 1995) could show that absolute pitch, which is the faculty to produce or identify a tone without a reference tone, is strongly related to the morphology of the left sided planum temporale (PT), a region pertaining to the auditory-related cortex and residing just beyond the primary auditory cortex (Steinmetz et al., 1989). The authors could not only show that the left PT has a larger surface area in musicians with absolute pitch in comparison to those without absolute pitch or laymen, but also that the volume of the left PT correlates with the age of commencement of musical training (Schlaug et al., 1995). The latter finding strongly militates in favour of the view that training intensity (or even the amount of training) is the critical variable that modulates the gray matter architecture of this perisylvian brain region. Furthermore, Amount and colleagues (Amunts et al., 1997) could show that professional musicians have a deeper central sulcus in the proximity of the hand

motor area (i.e., omega sign) in comparison to controls, and that this anatomical peculiarity correlates with the age of acquisition of musical training. Notably, this particular anatomical marker was shown to be more pronounced in the left hemisphere of violinists and to have a more bilateral representation in professional pianists. This can be associated with the fact that whereas playing violin places higher demands on the motor control of the left hand, playing piano more strongly rely on fine-graded bimanual movement adjustments.

The enduring influence of musical training on the human brain has not only been demonstrated by using anatomical techniques as shortly described above, but also by measuring brain functions with electrophysiological and neuroimaging techniques (Kraus et al., 2010; Munte et al., 2002). Meanwhile, a plethora of electrophysiological work found evidence for an increased sensitivity of the auditory system of professional musicians while processing timbre (Meyer, Baumann, & Jancke, 2006), pitch (Bidelman, Krishnan, & Gandour, 2011), rhythm (Geiser, Sandmann, Jancke, & Meyer, 2010), and duration (Marie, Kujala, & Besson, 2010) cues under attended or unattended experimental conditions. For example, by presenting violin and trumpet tones to professional violinists and trumpet players, Pantev and colleagues (Pantev et al., 2001) revealed increased brain responses to the familiar and more intensively trained sound attributes (i.e., timbre). Furthermore, by using a similar technique, Elbert and colleagues revealed that the cortical representation of the digits of the left hand of string players was larger than in control subjects (Elbert et al., 1995). Comparable results showing that musical training shapes the somatotopic organization of the brain were replicated by several other authors and also found in the domain of motor processing.

Beside professional musicians, to date several authors provide evidence that intensive training and experience in a particular domain influence the functional and structural organization of the human brain (Bezzola et al., 2011; Draganski et al., 2004; Maguire et al., 2000). Only to mention few awesome examples, Maguire and colleagues (Maguire et al., 2000) investigated professional taxi drivers from the city of London which have extraordinary abilities in the domain of spatial navigation. By performing MRI-based structural analyses, the authors revealed that the taxi driver group was characterized by an enhanced cortical volume in the posterior part of the right hippocampus in comparison to control subjects. Interestingly, the anatomical peculiarities of this specific brain region correlated with the amount of time spent as a taxi driver. A second example showing that a physical leisure activity can induce training-dependent anatomical changes was provided by Draganski and colleagues (Draganski et al., 2004). The authors could show that three month of juggle training resulted in an increased gray matter density in the human movement territory (i.e., V5) as well as in parts of the intraparietal sulcus; brain regions involved in the perceptual analysis of visual movement and in transferring retinotopic information to the motor system. Some years later the same research group provided evidence for the notion that not only motor- but also cognitive training has the faculty to influence the grey matter morphology of the human brain, as shown in a sample of medical student who learned for their final examination (Draganski et al., 2006). In conclusion, to date it is undisputed that the brain has the faculty to change itself as a function of exposure to a particular environment or training. The reorganization principles of the brain were described by different authors at the molecular, cellular, physiological or micro- and macro-anatomical level by using different techniques.

1.2. Simultaneous Interpreters as a Model for Neuroplasticity

In this chapter I will introduce a group of subjects which may be particularly appropriate for investigating functional and structural neuroplasticity as a function of language training as well as transfer effects originating from language training and extending to domains which were not specifically trained, namely professional simultaneous interpreters (SIs). Unlike professional musicians who normally begin with their training before the age of seven years (Schlaug et al., 1995), SIs acquire their professional skills as recently as in early adulthood. In fact, it should be considered that normally subjects enter to the interpreting college after the age of eighteen and spend several years of formal training in order to learn to translate a source language into a target language with a minimal time delay. Most notably, this sort of training not only implicates language translation per se, but is also associated with the development of exceptional cognitive, sensory-motor, and articulation skills. In fact, simultaneous interpreting places high demands on attention and working memory functions which are necessary for monitoring both the input and the output languages as well as to keep in mind the source language while formulating in the target language (Hervais-Adelman, Moser-Mercer, & Golestani, 2011; Rinne et al., 2000). Furthermore, professional simultaneous interpreting places high demands on sensory-to-motor coupling and motor-adjustments mechanisms, since linguistic inputs need to be almost simultaneously translated into an adequate output format by achieving an excellent pronunciation. Consequently, it results plausible to think that reorganization processes and transfer effects in SIs may originate as a consequence of all these performance requirements which are necessary for translating a source language into a target language at a professional level.

Even though to date a handful of electrophysiological (Grabner, Brunner, Leeb, Neuper, & Pfurtscheller, 2007; Proverbio, Leoni, & Zani, 2004; Proverbio, Adorni, & Zani, 2009) and neuroimaging (Rinne et al., 2000) studies investigated different cognitive aspects of interpreting, none of them examined neuroplasticity or transfer effects in those individuals. In turn I will provide a short overview of these previous studies. In a first EEG study, Proverbio and colleagues (Proverbio et al., 2004) investigated native Italian SIs during a semantic decision task (Italian and English, mixed and unmixed conditions) in which the subjects had to evaluate the congruency of the last word of visually presented sentences. This particular study was specifically designed to investigate code switching mechanisms in SIs. The main result of this work was that in the SIs group the electrophysiological N400 responses were significantly larger to L2 than L1 words, but only in the mixed condition. The fact that no effect of language was observed in the unmixed conditions, may suggest that the difference between L1 and L2 processing was not induced by a difference in proficiency, but rather associated with a different functional organization of the semantic integration systems in conjunction with the later age of acquisition of L2 compared to L1. In a follow-up EEG study, Proverbio and colleagues (Proverbio et al., 2009) investigated the temporal dynamics of brain responses within a group of SIs while they performed a visual letter-detection-task (within the native and later-acquired languages) not requiring semantic processing. The results of this EEG study complemented the findings of the previous study in that the authors could show differential electrophysiological responses in SIs between L1 and L2 processing. Since only L1 words were discriminated from pseudo-words at early processing stages (< 200 ms), results were interpreted as indicating a faster and more efficient lexical access to L1 than to later-acquired languages, regardless of proficiency.

A third EEG study was presented by Grabner and colleagues (Grabner et al., 2007) who explored event-related synchronisation (ERS) and de-synchronisation (ERD) during language translation in a sample of interpreting students. In order to measure the electrophysiological correlates of translation, the subjects were instructed to read visually presented high- and low-frequency English words and to translate them into the German language. The comparison of the translated high-frequency words with the low-frequency one yielded higher parietal theta ERS as well as frontal upper alpha ERD. Furthermore, the comparison between successfully translated low-frequency words and not translated words was associated with generally stronger ERD in the lower alpha band as well as with a larger left-hemispheric upper alpha ERD. These results provided first evidence for a sensitivity of alpha and theta ERS / ERD to lexical-semantic processing during language translation.

Currently, the only published neuroimaging study (PET) was conducted by Rinne and colleagues (Rinne et al., 2000) who investigated a group of SIs during simultaneous interpreting vs. repetition of auditory presented sentences. Results indicated that simultaneous interpreting was associated with an increased engagement of left prefrontal brain regions, which were previously shown to be related to lexical search, semantic processing, verbal working memory as well as attention functions (Rinne et al., 2000). Furthermore, the authors observed that the brain responses were clearly modulated by the direction of translation with more extensive brain responses during the translation into the non-native language, a task which is indeed considered to be cognitively more demanding.

1.3. The Contribution of Extra-Linguistic Brain Functions to Multilingual Speech Processing

The majority of work on multilingual speech processing has been conducted by investigating bilingual subjects. This particular group of subjects yielded important insides on the cortical representation and control of multiple languages. In this context, most of the neuroimaging and electrophysiological studies compared bilingual subjects with different levels of proficiency and ages of acquisition or even bilingual with monolingual subjects (Abutalebi & Green, 2007; Perani & Abutalebi, 2005). The main problem of suchlike comparisons is that the results are often contaminated by confounding variables (Perani et al., 1998). Beside the influence of these confounding, a detailed inspection of the meanwhile amount of literature published in the domain of multilingualism converges to the notion that language control is often dependent on brain regions situated outside the classical language areas (for an overview consider Abutalebi et al., 2007), this observation indicating that multilingual speech processing relies on more than just language representation per se. In fact, it should be considered that the practice of multiple languages has not only an impact on how linguistic information is represented in the human brain, but most notably also on how auxiliary cognitive processes (i.e., like attention, inhibition, working memory, switching mechanisms, etc.) are engaged in controlling the different languages (for an overview consider Abutalebi et al., 2007; Abutalebi, Tettamanti, & Perani, 2009). Furthermore, previous results even provide evidence for the notion that multilingual speech capacity is accompanied by plastic adaptations in regions involved in motor aspects of speech (Abutalebi et al., 2007; Hervais-Adelman et al., 2011) and in interhemispheric information transfer (Abutalebi et al., 2007; Coggins, Kennedy, & Armstrong, 2004; Hervais-Adelman et al., 2011). Whereas an optimal

tuning of brain regions supporting articulation is necessary for performing fine-graded motor adjustments while speaking in a foreign language, a more efficient interhemispheric transfer may be useful for enhancing the functional capacity of the frontal lobe, a brain region strongly involved in administrating cognitive control. Figure 1 provides an overview of the brain regions postulated to be fundamentally involved in exercising cognitive control and supporting language production in multilingual subjects.

Obviously, cognitive control mechanisms are closely linked to simultaneous interpreting as well (Christoffels, de Groot, & Kroll, 2006; Cowan, 2010; Daro & Fabbro, 1994; Rinne et al., 2000). Consequently, in a similar way as previously observed in proficient bilingual subjects (Abutalebi et al., 2007; Abutalebi et al., 2009; Bialystok, Craik, Klein, & Viswanathan, 2004; Costa, Hernandez, & Sebastian-Galles, 2008), one may anticipate that professional interpreting training has a strong influence on the brain characteristics of brain regions administrating cognitive control. Furthermore, due to the strong demands placed on articulation and sensory-to-motor mapping mechanisms during interpreting, one may expect that language expertise has an influence on brain regions involved in supporting the motor act of speech as well. All these training-related plastic adaptations can be expected by considering the processing requirements necessary for translating an input language into a target one, while attentively monitoring both the input language and its respective translation and at the same time inhibiting the articulation of the input language (Abutalebi et al., 2007; Abutalebi et al., 2009; Hervais-Adelman et al., 2011).

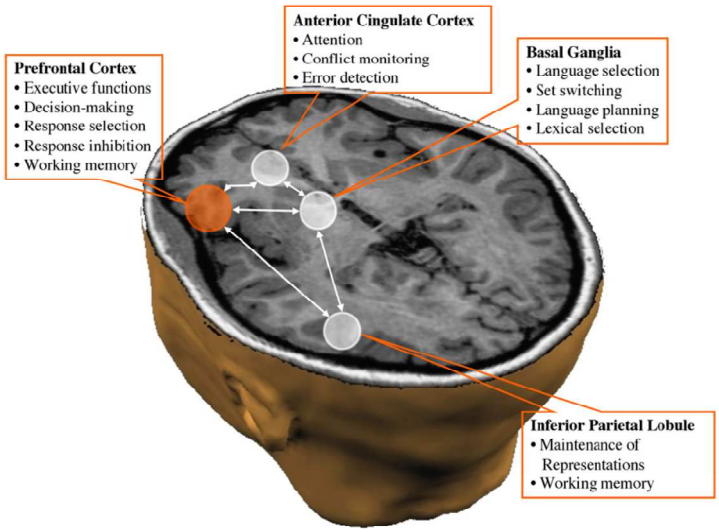

Figure 1: Schematic overview of brain regions involved in administrating cognitive control and language production in multilingual subjects (Abutalebi et al., 2007).

1.4. Transfer Effects

As shortly introduced in the previous chapter, meanwhile there is evidence pointing to the fact that expertise and training in a specific domain often entail behavioural and functional advantages in other domains which were not explicitly trained. A majority of evidence has been obtained by investigating transfer effects in professional musicians (Schlaug et al., 2005) or children undergoing short- or long-term musical training (Magne et al., 2006; Schlaug et al., 2005). In turn, I will shortly recapitulate the main findings describing transfer effects in musicians and afterwards I will address transfer effects in conjunction with language expertise.

Meanwhile, there is huge evidence for behavioural advantages as a function of musical training. For example, it has been shown that musical training facilitates visual-spatial abilities (Brochard et al., 2004), mental imagery (Aleman et al., 2000), mathematical abilities (Bilhartz et al., 1999; Gardiner, Fox, Knowles, & Jeffrey, 1996; Graziano, Peterson, & Shaw, 1999), symbolic or spatio-temporal reasoning (Gromko et al., 1998), as well as verbal memory functions (Ho, Cheung, & Chan, 2003). Furthermore, due to the intensive acoustic training professional musicians underwent, it is not surprising to find support for the fact that basic sound parameters like frequency, duration and intensity are differentially encoded by musicians and non-musicians (Kraus et al., 2010). Basing on this evidence more and more EEG (Besson, Schon, Moreno, Santos, & Magne, 2007; Marie et al., 2011; Schon, Magne, & Besson, 2004; Tervaniemi et al., 2009) and fMRI (Elmer et al., 2011; Oechslin, Meyer, & Jancke, 2010) studies were performed for investigating whether musical training facilitates speech processing as well. The results arising from these studies clearly show that professional musicians are more efficient at processing segmental (Elmer et al., 2011; Marie et al., 2011) as well as suprasegmental (Oechslin et al., 2010) speech information.

Even though to date the data collected in conjunction with musicianship indicate a clear link between musical training and perceptual and cognitive faculties in domains other than music processing, the question whether language expertise modulates neurocognition beyond the domain specifically trained has not yet been intensively addressed. Some evidence pointing in this direction arises from studies performed with bilingual and multilingual subjects. In this context, some work has linked language skills in proficient bilinguals with enhanced executive control functions

(Festman, Rodriguez-Fornells, & Munte, 2010), like attention (Costa et al., 2008) and inhibition functions (Bialystok et al., 2004; Festman et al., 2010), in comparison to monolingual subjects. Furthermore, it has been proposed that those bilinguals who have stronger language control abilities more likely show transfer effects to cognitive domains which were not explicitly trained (Festman et al., 2010), this pointing to a close intertwining of language expertise and cognition.

1.5. A Dual Stream Model of Speech Processing

A seminal model proposed by Hickok & Poeppel (Hickok & Poeppel, 2007) suggests that two segregated functional pathways are differentially engaged in supporting speech processing. A first ventral pathway, composed of bilateral processing streams and stretching from posterior perisylvian regions to the anterior temporal lobe, supports the extraction of segmental and suprasegmental acoustic cues and is involved in mapping sound-structure to meaning. A second left-dominant pathway extends from posterior perisylvian regions to the frontal operculum, supports auditory-to-motor transformations and articulation processes, and is assumed to play a relevant role for mapping sounds to articulation.

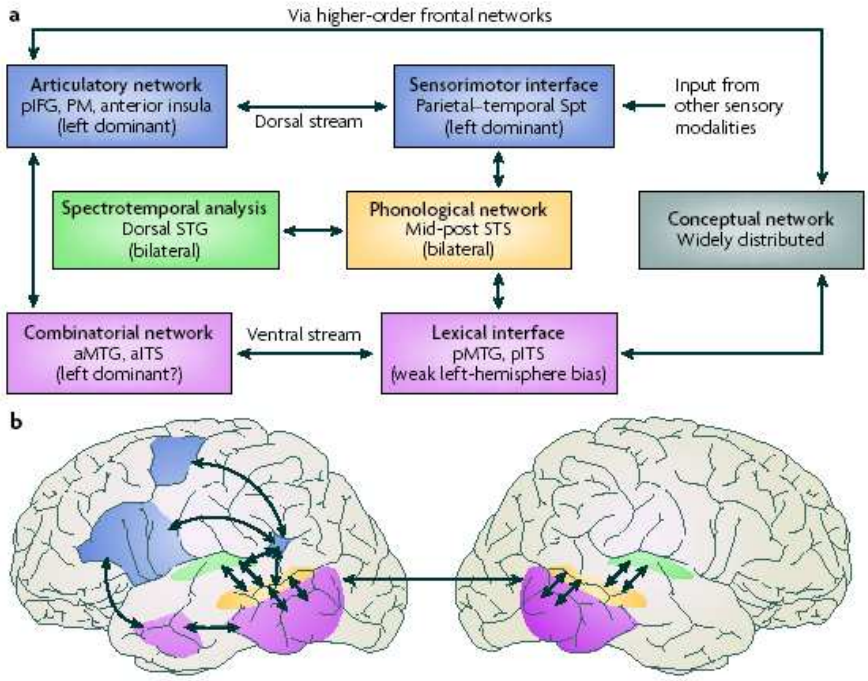

Figure 2: The dual stream model of speech processing proposed by Hickok and Poeppel (Hickok et al., 2007).

Recently, Saur and colleagues (Saur et al., 2008) tested the neuroanatomical basis of the dual stream model proposed by Hickok & Poeppel (Hickok et al., 2007) by combining the functional magnetic resonance imaging (fMRI) and diffusion tensor imaging (DTI) techniques. In order to separately engage the dorsal and ventral processing streams, the subjects performed two different language tasks, namely sub-lexical repetition and language comprehension. Results not only validated the dual stream model proposed by Hickok and Poeppel (Hickok et al., 2007), but also pointed to an anatomical segregation of the two processing streams. In particular, Saur and colleagues (Saur et al., 2008) provided evidence for the notion that the arcuate fasciculus and the superior longitudinal fasciculus can be considered as parts of the anatomical framework of the dorsal stream, whereas a part of the

extreme capsule was identified as the most probable anatomical candidate for the ventral processing stream.

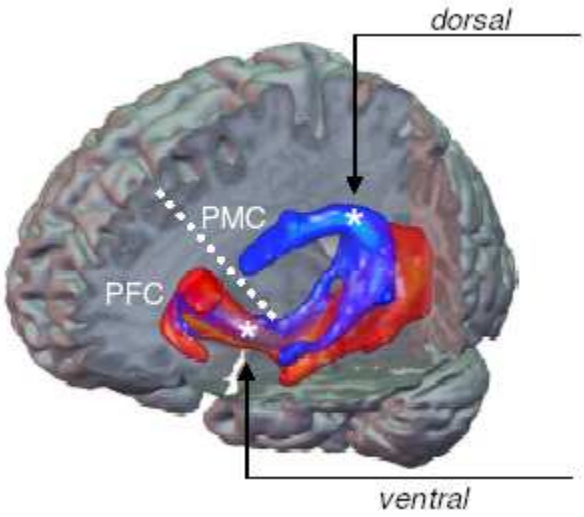

Figure 3: The anatomical substrate of the dual stream model presented by Saur and colleagues (Saur et al., 2008).

1.6. The Cortical Organization of Semantic Processing: an Overview

To date, umpteen neuroimaging studies have identified at least three regions involved in the computation of lexical-semantic information (Lau, Phillips, & Poeppel, 2008). These regions are the left posterior part of the middle temporal gyrus (MTG), the left anterior temporal cortex (ATC), and the left inferior frontal gyrus (IFG). All these brain regions were recently implemented in a neurofunctional framework by Lau and co-workers (Lau et al., 2008). This framework, which is visible in Figure 4, adverts to an amount of imaging data as well as on the investigation of patients with language comprehension deficits. In this context, Lau and colleagues postulated that the middle-posterior part of the left MTG mediates the long-term storage of information and the access to lexical-semantic representations. The left ATC, which

operates in cooperation with the angular gyrus (AG), has been suggested to support a higher-level integration of lexical-semantic inputs into larger units under construction, for example the syntactic structure, the propositional semantics and the discourse model. The IFG constitutes the third module of this framework and is supposed to be involved in the controlled selection and retrieval of lexical-semantic representations. The arrows depicted in Figure 4 represent pattern of functional connectivity.

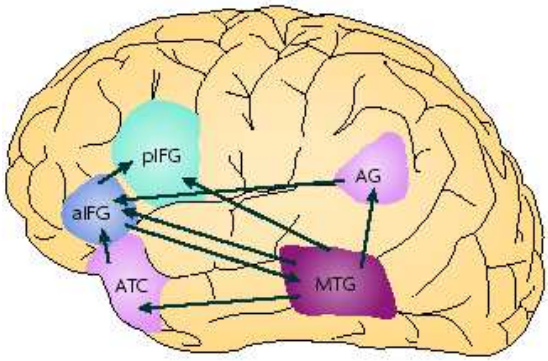

Figure 4: Schematic model of semantic processing (Lau et al., 2008). AG = angular gyrus, MTG = middle temporal gyrus, ATC = anterior temporal cortex, aIFG = anterior inferior frontal gyrus, pIFG = posterior inferior frontal gyrus.

Further evidence pointing to the functional dominance of left temporal, frontal and inferior-parietal brain regions for lexical-semantic processes arises from two seminal meta-analyses performed with fMRI data (Vigneau et al., 2006; Vigneau et al., 2011). Even though the functional contribution of the left hemisphere to lexico-semantic processing is in line with the framework presented by Lau and colleagues (Lau et al., 2008), the data provided by Vigneau and co-workers provide further evidence for the notion that lexical-semantic processing relies on distributed networks in both hemispheres. Since the functional contribution of the right hemisphere was mainly

observed in the context of language processing at the sentence level, the authors speculated about its role in processing contextual information. Figure 4 indicates the results of the meta-analysis performed by Vigneau and colleagues (Vigneau et al., 2011).

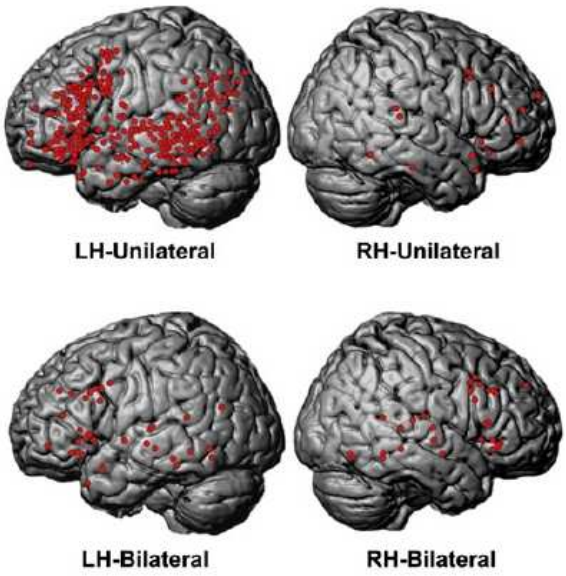

Figure 5: Left- (LH) and right-hemisphere (RH) distribution of unilateral and bilateral maxima of activations from a chosen set of neuroimaging studies performed in the context of lexico-semantic processing (Vigneau et al., 2011).

1.7. Language Production and Sound-to-Motor Mapping

Since the seminal work of Paul Broca on aphasic patients, the left inferior frontal gyrus in general and Broca's area in particular, were identified as brain regions which are strongly involved in supporting the motor act of speech (Ruff & Arbit, 1981; Schiff, Alexander, Naeser, & Galaburda, 1983). More recently, lesion studies performed with patients suffering from difficulties in speech articulation (Bates et al., 2003; Dronkers, 1996) have slightly modified this point of view. In fact, it has been shown that not only Broca's area, but also the left anterior insula is fundamental for the motor act of speech. This perspective was hardened by a further neuroimaging study presented by Wise and co-workers (Wise, Greene, Buchel, & Scott, 1999) in which the authors found evidence for the notion that the repetition of single words did not activate just Broca's area, but a more comprehensive motor-related network including the left anterior insula, the lateral premotor cortex, and the basal ganglia. Interestingly, the same study also revealed that the laft anterior insula is activated during both hearing and articulation, this result indicating that this region plays a pivotal role in the integration of sensory and motor information. A functional contribution of the left anterior insula to sensory-to-motor mapping mechanisms was confirmed by further authors (Mutschler et al., 2007; Mutschler et al., 2009), and shown to be restricted to overt task performance (Riecker, Ackermann, Wildgruber, Dogil, & Grodd, 2000).

A recent meta-analysis performed with fMRI data provided a more differentiated view of the brain regions involved in the motor act of speech (Eickhoff, Heim, Zilles, & Amunts, 2009). In this work, the authors re-evaluated neuroimaging data acquired in healthy subjects during verbal fluency tasks and identified a core motor network supporting speech production (see Figure 6). This network not only comprises Broca

pars opercularis and the left anterior insula, but also the basal ganglia, the cerebellum, the premotor cortex, as well as the primary motor cortex. Similar areas were also identified by functional and anatomical studies performed with patients suffering from specific clinical syndromes (Nestor et al., 2003) and language disorders (Jancke, Siegenthaler, Preis, & Steinmetz, 2007).

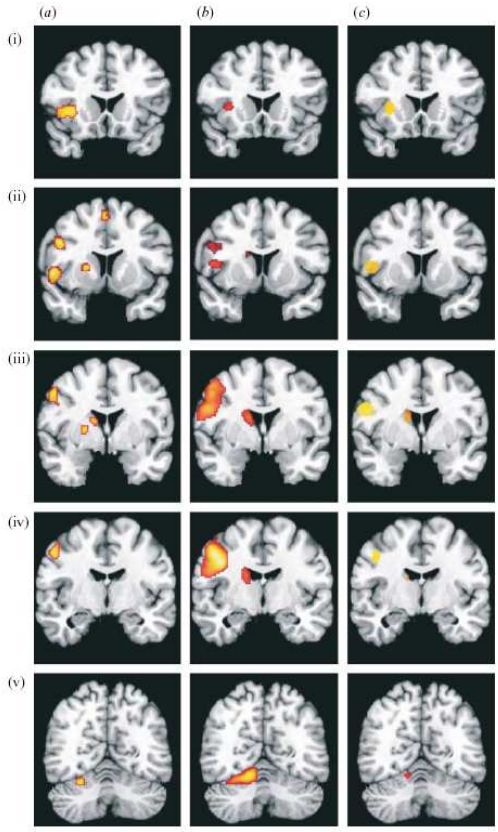

Figure 6: Localization of the core network involved in overt speech production as defined by (a) the meta-analysis of previous neuroimaging studies, (b) the fMRI random-effect group analysis, and (c) the location of the activation maxima for the individual subjects. (i) insula, (ii) BA 44, (iii) premotor cortex / caudate nucleus, (iv) primary motor cortex, and (v) cerebellum (Eickhoff et al., 2009).

2. METHODS

2.1. Methods: Electroencephalography (EEG), Functional Magnetic Resonance Imaging (fMRI), and Diffusion Tensor Imaging (DTI)

In the next sections, I will shortly introduce the three different research-techniques used for investigating brain plasticity and transfer effects in professional SIs. A first methodology used in the present work is called electroencephalography (EEG) and permits to directly measure the electrical activity of the brain by applying electrodes over the surface of the scalp. The advantage of the EEG technique is that it permits to measure brain functions with an excellent temporal resolution in the range of milliseconds. By contrast, the spatial resolution of this technique is relatively sparse and is situated in the range of cubic centimetres (Phillips, Rugg, & Friston, 2002). A second imaging technique that will be presented in turn is called functional Magnetic Resonance Imaging, or simply fMRI. The fMRI technique is a correlative method that enables to indirectly measure brain activity through metabolic and blood perfusion information. This technique permits to collect functional brain activation maps with a very high spatial resolution in the range of millimetres (Heeger & Ress, 2002). However, the temporal resolution of this methodology is markedly sparser than that of EEG and, situated in the range of seconds (Heeger et al., 2002). The third methodology used in this work is called Diffusion Tensor Imaging (DTI). DTI is a structural MRI-based technique which relies on the diffusion of water molecules along the principal fibre tracts in the brain. This technique is particularly fruitful in that it permits to trace white matter fibre bundles, to objectively determine their integrity or coherence, or to measure the volume of the single fibre tracts.

2.2. Electroencephalography (EEG)

The EEG technique was used for performing **study A**, entitled "*Simultaneous Interpreters as a Model for Neuronal Adaptation in the Domain of Language Processing".* The technical details concerning this methodology can be found in the original publication.

The EEG is the oldest technique that permits to directly measure the electrical activity of the brain. This technique was first developed by Hans Berger in the year 1924 and is today, thanks to improved mathematical implementations, a well established technique in the field of neuroscience. For measuring the electrical activity of the brain, electrodes are placed on the outer surface of the scalp and voltage fluctuations between each electrode and the reference electrode are recorded. The electrical signal measured at the surface of the scalp is supposed to reflect synchronous electrical activity originating from a large sample of nerve cells. The EEG technique can be used to investigate the neurophysiological correlates of cognitive or stimulus-driven brain functions as well as to determine the resting-state modus of the brain. Unlike the fMRI technique, the EEG is characterized by an excellent temporal resolution in the range of milliseconds and therefore gives important insides into the temporal dynamics of brain processes. Furthermore, due to novel mathematical applications, it is now possible to associate electrical potentials measured over the surface of the scalp with putative electromagnetic dipoles modelled inside the three-dimensional human brain. In the next section, the origin of the EEG signal will be shortly described.

2.2.1 The Origin of the EEG Signal

The EEG signal origins from synchronously activated nerve cells in the cerebral cortex. As a general organization principle, the neocortex is composed of piramid cells and apical dendrites which are oriented orthogonally to the surface of the brain. The dendrites play a fundamental role in carrying information arising from the axons to the nerve cells. Axons and dendrites are connected through junctions called synapses which are involved in the transmission of chemical or electrical signals between two or more cells. In general, the transmission of electrical signals between nerve cells can be described as follow: the action potential generated at the axonal hill of the pre-synaptic cell spreads along the axon and induces the realising of neurotransmitters at the synaptic cleft. These neurotransmitters pass the synaptic cleft and reach receptors in the post-synaptic membrane which change its microbiological structure and influence the flow of ions through the post-synaptic membrane. Consequently, it comes to a differential electrical potential distribution at the dendritic membrane between the intracellular and the extracellular space: while the intracellular space becomes more positive, the extracellular space becomes more negative. Furthermore, at the same time the potential differences at the soma of the piramid cells show exactly the inverse pattern. These different polarities of the electrical potentials at the dendritic membrane and at the soma can be considered as the origin of electromagnetic dipoles, which are oriented orthogonal to the surface of the brain, and can be measured by placing electrodes over the scalp (for a more detailed overview consider Ewert, 1998).

It should be considered that the currents originating from the brain are embedded in an environment of brain tissue and liquor cerebrospinalis, and therefore the induced current has to flow through all these media, as well as through the skull and scalp, in order to be measured by EEG electrodes. Since the current of a single nerve cell is small in magnitude and, by considering the considerable distance from the scalp surface, thousands of synchronously activated neurons are required for generating a measurable electrical signal at the surface of the scalp. Consequently, the EEG is only sensitive to a large number of simultaneously activated nerve cells.

2.2.2. Event-Related Potentials

The computation of event-related-potentials (ERPs) relies on the notion that brain responses measured on the surface of the scalp are time-locked to a particular sensory or cognitive event. For computing ERPs, these time-locked brain responses are averaged upon several events. This procedure is particularly fruitful in that brain responses are summed up and the random distributed noise (which is also present in the measured signal) can be extremely reduced. After this procedure, waveforms with a characteristic spatiotemporal dynamic are visible at each electrode, however with a discrepancy in latency, polarity, and magnitude. The present work focuses on a particular event-related response, namely on the N400 component. This ERP component has repeatedly been shown to be sensitive to lexical and semantic processing, and to have a maximal magnitude at centro-parietal scalp sides.

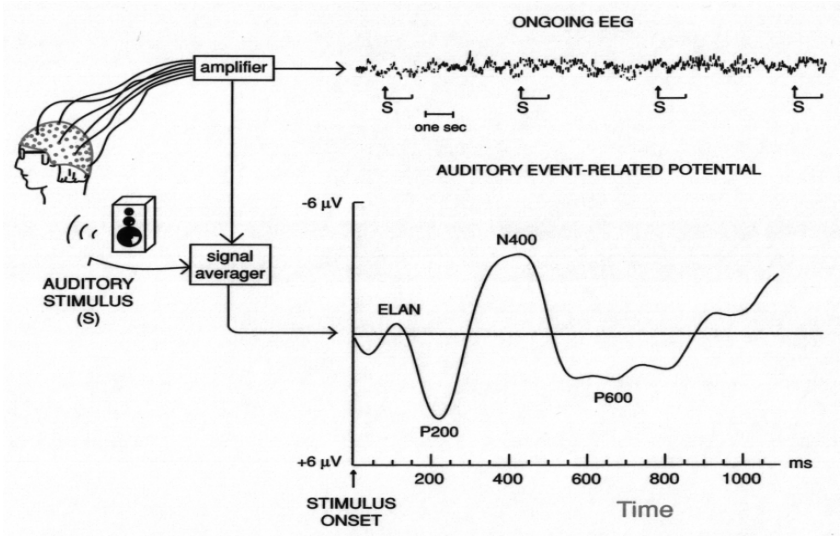

Figure 7: An overview of the EEG technique and the computation of event-related potentials (ERPs).

2.3. Functional Magnetic Resonance Imaging (fMRI)

The fMRI technique was adopted for performing **study C** entitled "*Intensive Language Training and Attention Modulate the Involvement of Fronto-Parietal Regions During a Non-Verbal Auditory Discrimination Task*". Since this technique has already been described in the methods section of the published work, here I will provide only a general overview of basic principles underlying this technique.

The fMRI signal constitutes an indirect measurement of brain activity and relies on the measurement of the Blood Oxygen Level-Dependent (BOLD) signal change, also called BOLD response. The BOLD response which is measured in the context of fMRI studies is contingent on the local blood perfusion properties of the brain as well as on the magnetic properties of oxy- (diamagnetic) and deoxyhemoglobin

(paramagnetic). Since deoxyhemoglobin is paramagnetic, it alters the magnetic resonance image signal. Consequently, deoxyhemoglobin can be considered as a form of endogenous tracer for measuring brain activity (Jäncke, 2005). In general, when a particular brain area is engaged in processing bottom-up or top down information, then the local blood flow is increased through different molecular and biochemical mechanisms with the intent to supply this brain area with new metabolic demands. The hemodynamic response starts with an increase of deoxyhemoglobin due to the local consumption of oxygen in an activated brain region (initial dip) and is initially not accompanied by a corresponding increase in blood flow. Afterwards, due to the increased metabolic demands of the engaged brain regions the blood flow increases, this leading to a change of the ratio between oxy- and deoxyhemoglobin. Since, the local concentration of oxyhemoglobin in the blood overruns that of deoxyhemoglobin, the ratio between oxy- and deoxyhemoglobin increases in the latency of 5-8 seconds; consequently an increase of the BOLD signal can be observed. Subsequently, the activated brain regions consume oxygen, this leading to a decrease in the ratio between oxy- and deoxyhemoglobin. This decreased ratio is associated with a reduction of the MR signal intensity to baseline; including a post-stimulus undershoot (Jäncke, 2005). In conclusion, by using particular sequences which are sensitive to changes in magnetic susceptibility, it is possible to measure the BOLD signal changes for each voxel in the human brain over time in comparison to a baseline.

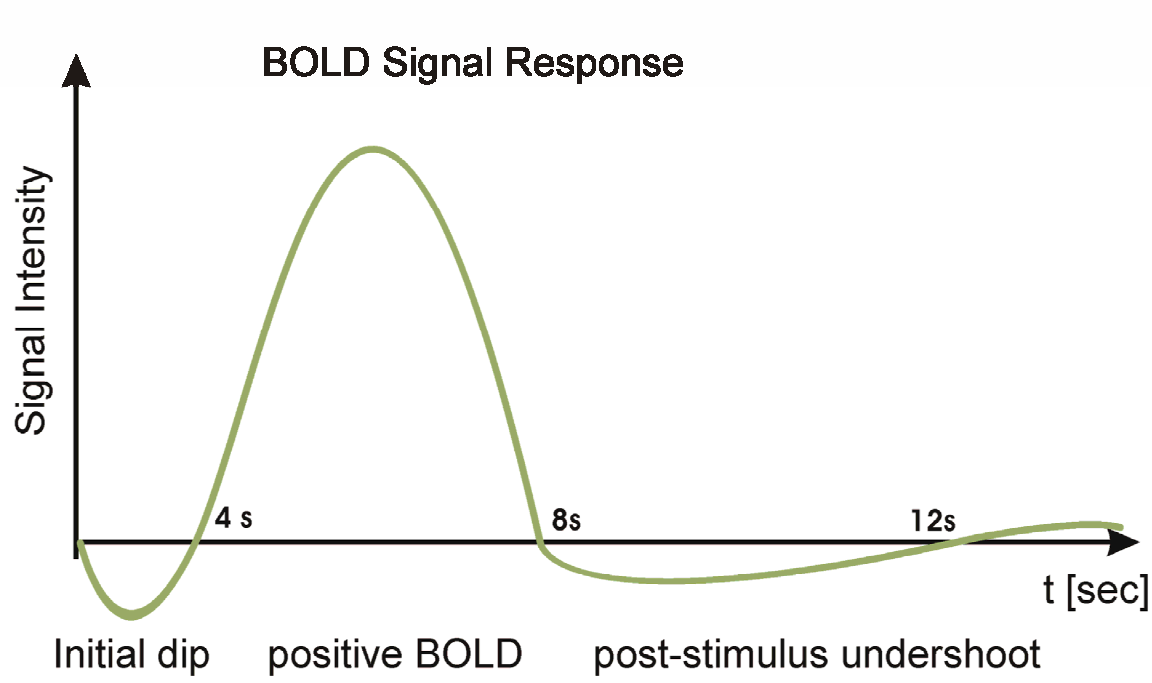

Figure 8: Time course of the BOLD signal change.

2.4. Diffusion Tensor Imaging (DTI)

The basic principles of the DTI technique were already addressed in the original publication of **study B**, entitled "*Differential Language Expertise Related to White Matter Architecture in Regions Subserving Sensory-Motor Coupling, Articulation, and Interhemispheric Transfer".* Therefore, in the present section I will only provide a short overview. The DTI technique bases on the diffusion of water molecules along white matter fibre tracts and permits to represent the tractography of fibre bundles as well as to detect differences in the integrity of the white matter architecture in healthy subjects as well as in patients. In particular, the Brown's movement of water molecules along the white matter pathways can be measured by adopting particular MR sequences and be quantitatively expressed by FA values (Fractional Anisotropy). The FA values express the directional dependence of the diffusion of water

molecules along the white matter fibre bundles in a numerical range from 0 (random diffusion) to 1 (aligned diffusion).

A previous methodological work (Mori & Zhang, 2006) provided a framework which is helpful for interpreting FA values collected with the DTI technique. In particular, Mori and Zhang proposed that reduced FA values can be associated with the following possibilities: 1) an increased diffusivity along the short axis (radial); 2) a decrease in diffusivity along the long axis (axial); 3) a combination of 1) and 2); or 4) with crossing fibres which lead to a decrease of FA values at the intersections. Furthermore, Beaulieu (Beaulieu, 2002) evidenced that not only myelinisation has an influence on the degree of anisotropy, but notably also the axonal membrane. Even though the DTI technique can provide interesting anatomical information in healthy and clinical populations, further methodological work is necessary for better comprehending the DTI results in a broader thematically context by integrating physiological, anatomical and functional data.

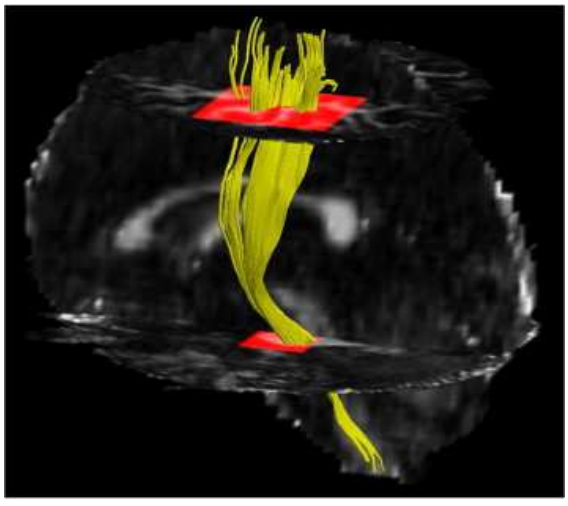

Figure 9: Basing on the DTI technique, a 3-dimensional model of the left corticospinal tract of a single subject is displayed (Imfeld et al., 2009).

3. PUBLISHED ORIGINAL RESEARCH ARTICLES

3.1. Study A: Simultaneous Interpreters as a Model for Neuronal Adaptation in the Domain of Language Processing.

Full Citation:

Elmer, S., Meyer, M., and Jäncke, L. Simultaneous interpreters as a model for neuronal adaptation in the domain of language processing. *Brain Research* 1317: 147-156, 2010.

3.1.1. Abstract

In the context of language processing, proficiency and age of acquisition have reliably been shown to have a strong influence on the functional and structural architecture of the human brain. The aim of the present EEG study was to examine the impact of language training as experienced by simultaneous interpreters (SI) on auditory word processing and to disentangle its influence from that of proficiency and age of acquisition. Eleven native German SIs and controls matched in L2 proficiency and age of acquisition were asked to judge whether auditory presented disyllabic noun pairs both within and across the German (L1) and English (L2) languages were either semantically congruent or incongruent. We revealed enlarged N400 responses in SIs while they detected incongruent trials both within the native (L1) and non-native (L2) language and also while they performed the task in the opposite direction as specifically trained (L1 to L2). These enlarged N400 responses in SIs suggest training-induced altered sensitivity to semantic processing within and across L1 and L2. The enlarged N400 responses we revealed in SIs to congruent noun pairs during the German-English condition (L1 to L2) may indicate that SIs could not benefit from

an L1 prime when the target was a L2 word, suggesting additional processing resulting from long-term backwards (L2 to L1) training.

BRAIN RESEARCH 1317 (2010) 147–156

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Research Report

Simultaneous interpreters as a model for neuronal adaptation in the domain of language processing

Stefan Elmer, Martin Meyer, Lutz Jancke*

Department of Neuropsychology, University of Zurich, Binzmühlestrasse 14/25, CH-8050 Zurich, Switzerland

ARTICLE INFO

Article history:
Accepted 16 December 2009
Available online 4 January 2010

Keywords:
Simultaneous interpreter
N400
Semantic decision task
Multilingualism
Plasticity
Language training

ABSTRACT

In the context of language processing, proficiency and age of acquisition have reliably been shown to have a strong influence on the functional and structural architecture of the human brain. The aim of the present EEG study was to examine the impact of language training as experienced by simultaneous interpreters (SI) on auditory word processing and to disentangle its influence from that of proficiency and age of acquisition. Eleven native German SI and controls matched in L2 proficiency and age of acquisition were asked to judge whether auditory presented disyllabic noun pairs both within and across the German (L1) and English (L2) languages were either semantically congruent or incongruent. We revealed enlarged N400 responses in SI while they detected incongruent trials both within the native (L1) and non-native (L2) language and also while they performed the task in the opposite direction as specifically trained (L1 to L2). These enlarged N400 responses in SI suggest a training-induced altered sensitivity to semantic processing within and across L1 and L2. The enlarged N400 responses we revealed in SI to congruent noun pairs during the German–English condition (L1 to L2) may indicate that SI could not benefit from an L1 prime when the target was a L2 word, suggesting additional processing resulting from long-term backwards (L2 to L1) training.

1. Introduction

To date, a plethora of studies have highlighted the exceptional efficiency of the human brain in changing its morphology and function due to long-term training in different domains (Maguire et al., 2000; Draganski et al., 2004, 2006). For example, various studies investigating professional musicians have clearly demonstrated mechanisms of neuronal reorganisation following intensive instrumental training that required the integration of multimodal sensory and motor information (Shahin et al., 2003; Munte et al., 2002; Jancke et al., 2000; Baumann et al., 2007).

In the domain of language processing, previous studies showed that the investigation of lexical–semantic networks is complicated by factors such as level of proficiency and age of acquisition (Proverbio et al., 2008; Elston-Guttler et al., 2005; Wartenburger et al., 2003). Whereas meanwhile it is undisputed that proficiency and age of acquisition strongly influence the functional and anatomical organisation of the human brain (Proverbio et al., 2004; Perani et al., 1998; Roux et al., 2004; Chee et al., 2004; Dehaene et al., 1997), the influence of long-term language training as experienced in SI on neuronal adaptation has yet to be addressed. Therefore, the aim of the present study was to examine the impact of long-

* *Corresponding author*. Fax +41 44 635 7409.
E-mail addresses: s.elmer@psychologie.uzh.ch (S. Elmer), m.meyer@psychologie.uzh.ch (M. Meyer), l.jancke@psychologie.uzh.ch (L. Jancke).

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doi:10.1016/j.brainres.2009.12.052

term language training on single word processing and to disentangle its influence from that of proficiency and age of acquisition.

An interesting approach to examine training-related plasticity in the domain of language processing is the investigation of individuals with a similar age of acquisition and proficiency in more than one language but differing in the amount of training in a particular domain. To date, only two electrophysiological studies have investigated SI and none of them applied auditory presented material as stimuli or compared SI with matched controls in order to uncover training-related neuronal adaptation. In a first study, Proverbio et al. (2004) explored native Italian SI and monolingual control subjects during a semantic processing task (Italian and English, mixed and unmixed conditions) in which the subjects had to evaluate the congruency of finally presented words in the context of sentence processing. By comparing the N400 responses to the visual presentation of Italian sentences (L1), no main effect of groups was found, except for a tendency for SI to respond slower than controls. Moreover, in the SI group, the N400 responses were significantly larger to L2 than L1 words, but only in the mixed condition. The fact that no effect of language was observed in the unmixed conditions, may suggest that the differential processing between L1 and L2 was not related to a difference in proficiency, but rather to a different functional organisation of semantic integration systems due to the later age of acquisition of L2 compared to L1. Unfortunately, this study was conducted with interpreters that knew at least four languages (with good Italian and English skills) and with monolingual controls that only spoke Italian, the study therefore not being informative to reveal training-induced plastic adaptations. In a follow-up study, Proverbio et al. (2008) investigated the temporal dynamic of brain responses within a group of SI while they processed a visually presented letter-detection-task (within the native and later-acquired languages) not requiring semantic processing. Precisely because only L1 words were discriminated from pseudo-words at an early processing stage (<200 ms), it was interpreted as a faster and more efficient access to lexicon for L1 than for later-acquired languages, regardless of proficiency. The sole imaging study (PET) (Rinne et al., 2000) performed within a group of SI during simultaneous interpreting vs. repetition of auditorily presented sentences, showed that interpreting strongly involved the left prefrontal cortex, a region previously shown to be related to lexical search (Whitney et al., 2009), semantic processing (Blacker et al., 2006) and verbal working memory functions (Rodriguez-Jimenez et al., 2009). In the absence of any studies investigating training-related adaptation in SI and controls with a comparable proficiency and age of acquisition across more than one language, we addressed this novel issue in a preliminary study.

Previously, lexical–semantic processing has been investigated both within and across different languages by examining whether processing is facilitated when a word is presented after its translation (Jin, 1990; Cristoffanini et al., 1986; Kirsner et al., 1984). In this context, it was shown that when target words are preceded by semantically related words, behavioural responses are usually faster in tasks involving lexical decisions (Meyer and Schvaneveldt, 1971) or semantic judgements (Phillips et al., 2006; Deacon et al., 1995, 1991). Meanwhile, it is established that (1) the N400 component is selectively sensitive to lexical–semantic processing (Moreno and Kutas, 2005; Friederici et al., 2004; Ye et al., 2006), (2) the magnitude of the N400 component is smaller for primed than unprimed words (Kutas and Hillyard, 1980) and (3) that a mismatch between the meanings of two sequentially presented words produces more negativity in the associated N400 component (Kojima and Kaga, 2003).

Surprisingly, to date only few EEG studies have adopted auditory stimuli to investigate lexical–semantic processing at the level of single noun presentation (Phillips et al., 2006; Sinai and Pratt, 2002; Radeau et al., 1998; Perrin and Garcia-Larrea, 2003; Kotz et al., 2002). Some of these studies (Radeau et al., 1998; Perrin and Garcia-Larrea, 2003) were conducted within the native language and evidenced that semantically related words are associated with smaller N400 amplitudes compared to unrelated ones. Other studies (Phillips et al., 2006; Sinai and Pratt, 2002) compared lexical–semantic processing between the native language and later acquired languages. One particular EEG study (Sinai and Pratt, 2002) investigated the N400 responses in native Hebrew speakers (L1) that acquired English later in life (L2) by presenting to the subjects pairs of auditory stimuli in Hebrew and English (words and pseudo-words) in the context of a lexical decision task. The results of this study showed that the N400 amplitudes were larger for pairs that included second language pseudo-words, were intermediate for pairs that included pseudo-words from the first language and were smallest when both stimuli were words. In a different linguistic context, namely that of early bilingualism, Phillips et al. (2006) examined English (L1)–French (L2) bilinguals. The authors could show that repeated within-language presentations of a word and within-language change in meaning elicited similar N400 effects in both L1 and L2. Moreover, for translated words, a change in language from L1 to L2 elicited similar N400 magnitudes as did a within-language change in meaning in L1, thus suggesting that conceptual information was not available on-line in early bilinguals for L1 to L2 translations. By contrast, the presence of minimal N400 effects for L2 to L1 translation indicated that conceptual information was available on-line for backwards translations (Phillips et al., 2006).

In the domain of language processing, SI represent an ideal group for studying the function and structure of the human brain in conjunction with training-related plastic adaptations and expertise. This approach is novel in that it enables the investigation of plasticity while controlling for other variables, such as age of acquisition and proficiency. The translation skills developed through a specific training constitute the main aspect that differentiates professional SI from other multi-lingual subjects. For this reason, we investigated professional SI and controls matched in proficiency and age of acquisition by comparing electrophysiological responses to semantically congruent and incongruent noun pairs between the two groups.

The aim of the present study was to evaluate the impact of professional language training on auditory word processing and to disentangle the influence of training from that of proficiency and age of acquisition. In the present study, we hypothesised (1) that SI will differ from matched controls

during single word processing in the professionally practiced language direction (L2 to L1). Furthermore, we addressed the following questions: (2) Do these differential processing modes also extend to forward translation (L1 to L2)? (3) Does professionally trained switching between two languages modulate word processing within the single languages? (4) Are neuroplastic adaptations related to both the congruent and incongruent conditions?

2. Results

2.1. *Proficiency, age of L2 acquisition and amount of L2 exposure*

Language proficiency (listening, grammar and vocabulary) was assessed as an ordinal scaled variable (see methods) and therefore compared non-parametrically between the groups (Mann-Whitney test). Two SI abstained from language testing. The two missing language assessments are due to the fact that two of the measured subjects worked for the European Union and were in Switzerland only for a short time. It was not possible to perform a measurement of language skills at a later time.

The outcome of these comparisons indicated that the groups did not significantly differ in proficiency (grammar: Mann–Whitney $Z=-.041$, $p=.96$; listening: Mann–Whitney $Z=-.401$, $p=.68$; vocabulary: Mann–Whitney $Z=-.458$, $p=.64$). Furthermore, the analysis of age of L2 acquisition (*t*-test for independent samples) did not reveal significant differences among groups ($t(20)=-.580$, $p=.569$, two tailed). Hence, we assumed a similar proficiency and age of L2 acquisition in both groups.

In order to rule out the possibility that the significant electrophysiological group differences were related to a different amount of L2 exposure since childhood, we non-parametrically compared (Mann–Whitney test, two tailed) the subjective data (E % 7–14, E % 15–18, E % 18–22, E % 22–30, E % 30 years until now) between the two groups. Since none of these comparisons reached significance, it is unlikely to assume that this variable influenced brain responses.

2.2. *Error scores and reaction times*

The evaluation of error scores and reaction times between the two groups was performed through separate 2 (groups, G)×4 (language directions, LD) repeated-measure ANOVAs. The analysis of error scores revealed significant LD and G effects (LD: $F(1, 20)=35.42$, $p<.001$, $eta^2=1$; G: $F(1, 20)=9.50$, $p<.01$, $eta^2=.83$) as well as a significant LD × G interaction (LD×G: $F(1, 20)=5.93$, $p<.05$, $eta^2=.64$). Post hoc *t*-tests for independent samples reached significance in the language direction EE (EE: $t(20)=-3.63$, $p<.01$, two–tailed). Fig. 1 illustrates that controls committed significantly more errors performing semantic decisions within L2. The ANOVA performed on reaction times data revealed a main effect of LD (LD: $F(1, 20)=4.76$, $p<.05$, $eta^2=.547$). The main LD effect was related to longer reaction times in both groups during the EE condition (see Fig. 1).

In order to inspect whether the longer reaction times and the differential error scores between the groups were related to a lower word frequency in the target words of the EE list, we further performed non-parametric statistical analyses (Kruskal–Wallis test). The results of these analyses revealed that the target words from the EE list had a significant lower frequency than those from the GG (Chi-Square (1)=5.717, $p=.017$, two tailed), GE (Chi-Square (1)=6.417, $p=.011$, two tailed) and EG (Chi-Square (1)=9.482, $p=.002$, two tailed) lists. All other comparisons are not reached significance. These results suggest that the longer reaction times in both groups during the EE condition and the greater amount of errors in the control group during this condition were related to more infrequent targets words in the EE condition.

2.3. *N400 responses to incongruent noun pairs*

The second incongruent word of the pair elicited a typical N400 response characterised by a centro-parietal current distribution in both groups, as seen in Fig. 2. Due to movement artefacts, we eliminated some trials from the ERP analysis. The mean percentage of eliminated trials is listed in turn: SI, GG (4.8 %); C, GG (6.2 %); SI, EE (5.2 %); C, EE (4.8 %); SI, GE (6.5 %); C, GE (5.4 %); SI, EG (3.3 %); C, EG (3.3 %).

The electrophysiological responses to incongruent noun pairs were subjected to repeated-measure ANOVAs. With this purpose in mind, we computed 8 (TW)×2 (G) ANOVAs with TW as within subject factor and G as between-subject factor, one for each LD. These analyses revealed differential N400 responses in three of the four language directions, namely GG, EE and GE.

The statistical analysis performed within the native language direction (GG) revealed a TW×G interaction and a

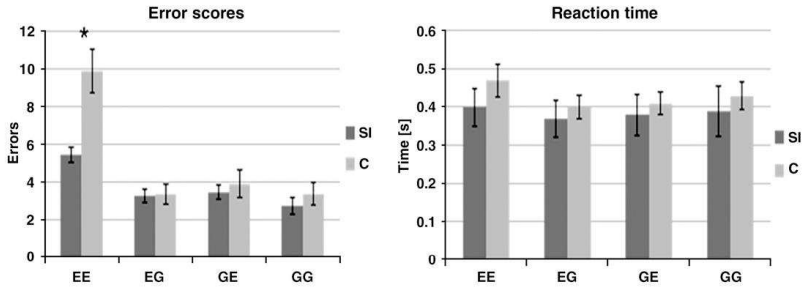

Fig. 1 – Mean amount of error scores and mean reaction times of both groups separately for each language direction. **$p<.01$.

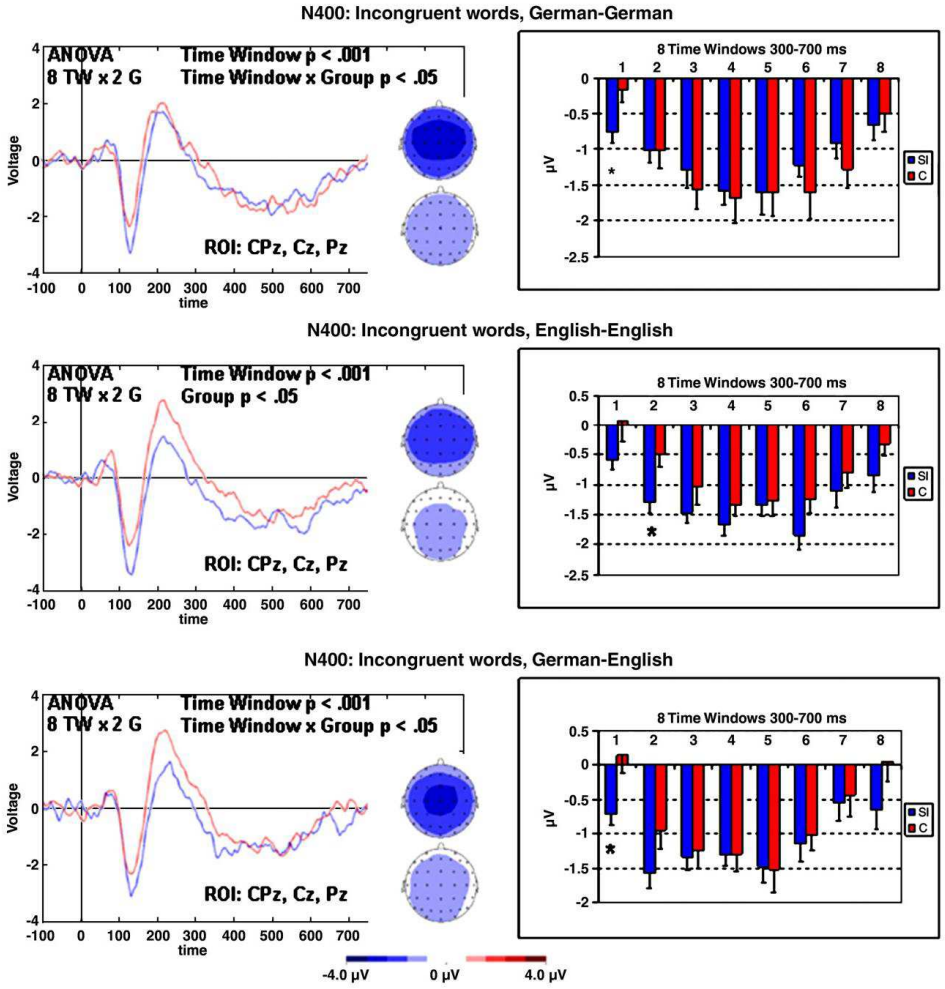

Fig. 2 – Responses to incongruent nouns for both groups. The data refer to voltage values within an ROI. The x-axis shows time course in milliseconds (ms), the y-axis depicts mean voltage values in μV. Blue = SI, red = controls. The figure also reports mean amplitudes in eight consecutive time windows for the EE, GG and GE language directions. 1 = 300–350 ms, 2 = 350–400 ms, 3 = 400–450 ms, 4 = 450–500 ms, 5 = 500–550 ms, 6 = 550–600 ms, 7 = 600–650 ms, 8 = 650–700 ms. Red bars = controls, blue bars = SI. *$p < .05$. Scalp maps between 300 and 700 ms are shown, the upper map refers to SI and the lower to controls.

main TW effect (GG: TW $F(1, 20) = 41.831$, $p < .001$, $eta^2 = 1$; TW × G $F(1,20) = 5.640$, $p < .05$, $eta^2 = .618$). Post hoc comparisons (*t*-tests for independent samples) reached significance in the time window 300–350 ms (300–350 $t(20) = -2.408$, $p < .05$, two tailed). The analysis within the non-native language direction (EE) revealed main TW and G effects (EE: TW $F(1, 20) = 82.170$, $p < .001$, $eta^2 = 1$; G $F(1,20) = 4.509$, $p < .05$, $eta^2 = .524$). Post hoc *t*-tests depicted significance in the time window 350–400 ms (350–400 $t(20) = -2.787$, $p < .05$, two tailed). The analysis of incongruent GE noun pairs yielded a significant TW effect and a TW × G interaction (GE: TW $F(1,20) = 47.908$, $p < .001$, $eta^2 = 1$; TW × G $F(1,20) = 6.211$, $p < .05$, $eta^2 = .660$). Post hoc comparisons (*t*-tests) yielded significance in the TW 300–350 ms (300–350 $t(20) = -2.786$, $p < .05$, two tailed). The statistical comparison of unrelated EG nouns revealed a main TW effect (TW $F(1,20) = 21.524$, $p < .001$). Table 1 shows an overview of the significant results.

In summary, SI showed enlarged responses to incongruent noun pairs during early N400 processing stages both within and across L1 and L2, but not in the language direction

Table 1 – N400 responses to incongruent noun pairs.

ANOVAs	Language direction	Factor	*df*	F-value	*p*-value
8×2	EE	TW	1	82.17	<.001
		G	1	4.509	<.05
8×2	EG	TW	1	21.524	<.001
8×2	GE	TW	1	47.908	<.001
		TW×G	1	6.211	<.05
8×2	GG	TW	1	41.831	<.001
		TW×G	1	5.64	<.05

The table shows the significant results of the ANOVAs for the N400 responses to incongruent noun pairs. TW, time window; G, group.

Table 2 – N400 responses to congruent noun pairs.

ANOVAs	Language direction	Factor	*df*	F-value	*p*-value
8×2	EE	TW	1	12.177	<.01
8×2	EG	TW	1	18.282	<.001
8×2	GE	TW	1	18.708	<.001
		G	1	5.994	<.05
8×2	GG	TW	1	19.269	<.001

The table shows the significant results of the ANOVAs for the N400 responses to congruent noun pairs. TW, time window; G, group.

professionally practiced. Fig. 2 and Table 1 show an overview of the results.

2.4. *N400 responses to congruent noun pairs*

The second congruent nouns of the German–English condition elicited a negative component in the N400 time window, but only in the SI group. This negative wave was characterised by a frontal negativity, as visible in the scalp map of Fig. 3. Due to movement artefacts, we eliminated some trials from the ERP analysis. The mean percentage of discharged trials is listed in turn: SI, GG (5.4 %); C, GG (5 %); SI, EE (6.6 %); C, EE (5.1 %); SI, GE (4.4 %); C, GE (6.1 %); SI, EG (2.7 %); C, EG (5.2 %).

The N400 responses to congruent nouns were subjected to repeated-measure ANOVAs. We computed 8 (TW)×2 (G) ANOVAs with TW as within subject factor and G as between-subject factor, one for each LD. This analysis revealed a main TW effect in all four language directions (GG: TW $F(1, 20)=19.269$, $p<.001$, $eta^2=.986$; EE: TW $F(1, 20)=12.177$, $p<.01$, $eta^2=.913$; EG: TW $F(1, 20)=18.282$, $p<.001$, $eta^2=.982$, GE: TW $F(1,20)=18.708$, $p<.001$, $eta^2=.984$). In addition, statistical analysis performed in the GE language direction (L1 to L2) revealed a significant G effect (G $F(1,20)=5.994$, $p<.05$, $eta^2=.644$). Post hoc comparisons (t-tests) reached significance in 4 consecutive time windows (300–350 $t(20)=-2.340$, $p<.05$, two tailed; 350–400 $t(20)=-3.411$, $p<.01$, two tailed; 400–450 $t(20)=-2.430$, $p<.05$, two tailed; 450–500 $t(20)=-2.089$, $p<.05$, two tailed). Table 2 shows an overview of the significant results.

In summary, the SI group showed enlarged N400 responses while hearing congruent nouns in the opposite direction (L1 to L2) to that professionally trained.

2.5. *N400 responses within the SI group*

Since the SI we measured differed in the amount of years of work experience (see Table 3), we non-parametrically (Mann–Whitney test) compared the less experienced SI (subjects 2, 5, 6, 8, 9, 10, 11) with the more experienced SI (subjects 1, 3, 4, 7). With this purpose in mind, we compared the 8 TW between the two groups for each LD (EE, GG, GE, EG) and condition (congruent/incongruent). The analyses of the mean N400 amplitudes revealed a significant difference between the two groups in the incongruent EE condition only (300–350 ms, $U(11)=2$, $Z=-2.268$, $p=.023$, two tailed). In particular, the less experienced SI showed more negative mean amplitudes than the SI with many years of work experience. Since this was the only significant difference we revealed within the SI group, our data may suggest that the differential electrophysiological responses between the SI and control groups are more likely

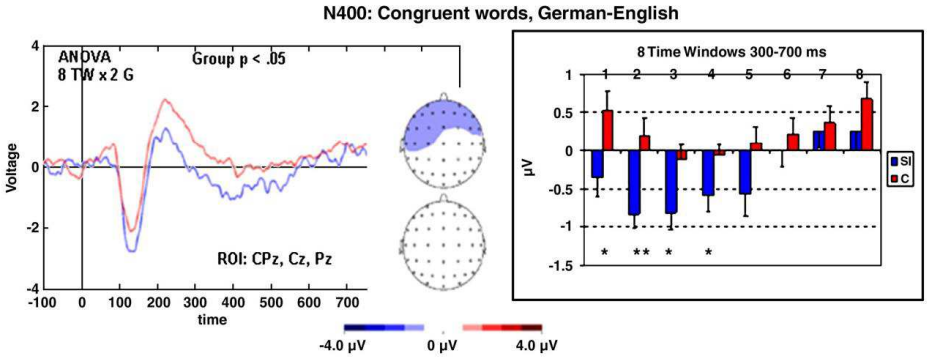

Fig. 3 – Responses to congruent nouns for both groups. The data refer to voltage values within an ROI. The x-axis shows time course in milliseconds (ms), the y-axis depicts mean voltage values in µV. Blue = SI, red = controls. The second plot reports mean amplitudes in eight consecutive time windows for the GE language direction. 1 = 300–350 ms, 2 = 350–400 ms, 3 = 400–450 ms, 4 = 450–500 ms, 5 = 500–550 ms, 6 = 550–600 ms, 7 = 600–650 ms, 8 = 650–700 ms. Red bars = SI, blue bars = controls. *$p<.05$, **$p<.01$. Scalp maps between 300 and 700 ms are shown; the upper map refers to SI and the lower to controls.

Table 3 – Biographical and behavioural data.

Variables	Subjects																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Age	46	40	44	42	34	40	48	35	26	33	28	46	42	33	47	38	38	40	37	40	48	37
Age of acquisition of E	12	16	14	10	11	14	14	12	6	14	13	12	15	16	11	12	13	12	13	13	14	11
Proficiency level of E																						
Listening	c1	c1	c1	c1	c1		c1		c2	c1	b2	c1	c1	c2	b2	c1	c1	c2	c1	c1	c1	b2
Vocabulary	b2	c1	c2	c2	b2		c1		c2	c1	c1	c1	c1	c1	b2	c2	c1	c1	c2	c2	b2	c1
Grammar	b2	c1	c1	c2	b2		c1		c2	c1	b2	c2	c2	b2	b2	c2	b2	c2	b2	c2	b2	b2
Actual amount of E exposure per week in hours	5	1	8	16	4	5	5	25	20	15	4	2	2	4	2	2	2	5	5	4	1	15
% of E exposure since childhood																						
E % 0–6 years	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E % 7–14 years	10	0	0	5	1	5	5	20	10	0	8	10	0	0	3	1	5	5	10	0	0	10
E % 15–18 years	20	1	20	10	1	10	20	30	70	10	15	10	10	5	3	20	10	10	20	1	20	10
E % 18–22 years	20	1	20	20	1	60	25	30	80	10	40	25	10	25	5	9	20	20	60	5	0	10
E % 22–30 years	10	10	20	20	5	70	30	50	30	20	30	20	10	15	5	9	20	10	20	10	0	60
E % 30 years until now	5	5	10	20	5	60	10	50	20	20	5	10	10	15	5	9	15	10	30	10	1	25
Years of work experience as SI	25	7	20	17	4	10	23	8	1	3	2											
Amount of hour per week SI medially labour	4	4	16	2	2	11	10	2	2	2	30											

The table reports biographical and behavioural data of the measured subjects. The first 11 subjects listed were SI. The amount of English exposure refers to every kind of preoccupation with the English language (reading, watching television, discussions) but not listening to English music.

related to the specific training during the SI education rather than to the amount of years of experience.

3. Discussion

3.1. *General discussion*

A number of previous studies have shown that intensive training is associated with significant plastic adaptations evident in modifications of the brain's neuronal underpinnings, strengthening of neuronal connections, and alteration of macro-anatomical configuration (Draganski et al., 2004; Munte et al., 2002; Jancke et al., 2000; Baumann et al., 2007; Maguire et al., 2000; Jancke, 2009). Several of these studies investigated professional musicians and clearly demonstrated mechanisms of neuronal reorganisation following intensive sensory-motor training (Shahin et al., 2003; Munte et al., 2002; Jancke et al., 2000; Baumann et al., 2007). Similar to these studies with professional musicians, we evaluate the SI's brain as a model for training-related reorganisation in the domain of language processing, and we demonstrate that the intensive training experienced by SI is accompanied by functional adaptations in accessing lexical–semantic information. The examination of SI and matched controls is particularly fruitful in that it enables the investigation of the impact of long-term training on language processing and the differentiation of this influence from that of proficiency and age of acquisition. With this purpose in mind, we used an electrophysiological approach (EEG/N400) in combination with a semantic decision task, involving the detection of semantically congruent and incongruent noun pairs within and between L1 (German) & L2 (English). Our data clearly show differential N400 responses between the two groups in the incongruent and in the congruent conditions, but not in the language direction professionally trained (L2 to L1). We revealed enlarged N400 responses in SI while they detected incongruent trials both within the native (L1) and non-native (L2) language and also while they performed the task in the opposite direction as specifically trained (L1 to L2). These enlarged N400 responses in SI suggest a training-induced altered sensitivity to semantic processing within and across L1 and L2. The enlarged N400 responses revealed in SI to congruent noun pairs during the German–English condition (L1 to L2) may indicate that SI could not benefit from an L1 prime when the target was a L2 word, suggesting additional processing resulting from long-term backwards (L2 to L1) training.

3.2. *Behavioural results*

The behavioural results demonstrated a comparable L2 proficiency in the two groups. However, the control subjects committed more errors than SI in judging the semantic relatedness of EE noun pairs, and the two groups showed significantly longer reaction times during this condition (see Fig. 1). To determine whether these longer reaction times and the differential error scores between the two groups were associated with word frequency of the EE target words, we performed post hoc analyses. This statistical approach revealed that the target words from the EE condition had a significantly lower frequency than those from the GG, GE and EG conditions, suggesting that the longer reaction times in the two groups and the greater amount of errors in the control subjects were related to more infrequent targets words in the EE condition. Since the two groups did not differ in L2 proficiency but did show differential error scores in the EE condition, we favour a careful interpretation of the electrophysiological data collected in the EE condition. The comparisons of RT did not yield significant group differences, probably because we inserted a delay after the presentation of the second noun in the pair and response selection in order to avoid response-related activations in the N400 time window.

3.3. Differential N400 responses to congruent trials

Our electrophysiological data revealed significant group differences while identifying German prime- and English target words as synonyms (see Fig. 3). These differential responses were associated with enhanced N400 deflections in the SI group between 300 and 500 ms after stimulus presentation.

The congruent conditions of this study can be regarded as a semantic priming task (Elston-Guttler and Gunter, 2009; Uusvuori et al., 2008), since such priming is seen to be a measure of the strength of lexical–semantic relationships among words. Posner and Snyder (1975) postulated in a theoretical framework that activation spreads from a particular node in lexical–semantic memory that represents the prime word to other adjacent nodes that represent related words. In the context of electrophysiology, previous studies (Kutas and Hillyard, 1980) undoubtedly showed that the magnitude of the N400 component is smaller for primed than unprimed words and that a mismatch between the meanings of two sequentially presented words produces more negativity in the associated ERPs (Kojima and Kaga, 2003).

Since SI elicited enhanced N400 responses while hearing congruent nouns in the direction opposite (L1 to L2) to that usually trained (L2 to L1), our data suggest that SI could not fully benefit from a German prime word when the target was an English word. These enhanced N400 responses in the SI group may be associated with extra processing resulting from long-term backwards (L2 to L1) translation training. This means that continuous L2 to L1 training in SI makes task performance in the opposite direction (L1 to L2) more difficult for them than it is for the controls. Our results are in line with two previous studies (Rinne et al., 2000; Proverbio et al., 2004) that independently investigated brain responses within a group of SI and found evidence for asymmetrical switching costs, which were particularly evident in the L1 to L2 direction. The authors consistently proposed that language switching might affect semantic integration processes when an item of the weaker L2 language is encountered, since translation into the non-native language is considered a more demanding task (Rinne et al., 2000). However, these two studies did not explicitly compare switching mechanisms between SI and matched control subjects and therefore the results only provide information on switching mechanisms in SI. Our results supplement these findings and show that the intensive L2 to L1 training experienced by SI results in additional processing costs (compared with controls) when the opposite language direction (L1 to L2) is encountered. This finding is relevant in that it shows that training-related functional reorganisation takes place independently from the influence exerted by age of acquisition and proficiency.

3.4. Differential N400 responses to incongruent trials

In the present study, we found differential N400 amplitudes between the two groups while subjects performed incongruent GG, EE and GE trials, but not while they detected incongruent trials in the professionally trained language direction (L2 to L1) (see Fig. 2). These differential responses were reflected in enhanced N400 amplitudes in the SI group between 300 and 400 ms.

It is now well established that a mismatch between the meanings of two sequentially presented words or words which are incongruent with the context produce more negativity in the associated ERPs (Kojima et al., 2003), this being associated with more processing resulting from the difficulty of retrieving stored conceptual knowledge related to a word (Van Petten and Luka, 2006). Since we revealed enhanced N400 amplitudes in the SI group while processing incongruent trials in the GG, EE and GE direction, our data suggest a differential functional organisation of lexical–semantic processing between the two groups. One particular EEG study (Midgley et al., 2009), which focussed on language processing in second language learners and early bilingual subjects during reading single nouns, showed that the N400 amplitude is modulated by proficiency with more proficient subjects showing enhanced negativity in the associated ERPs. Considering that the control subjects committed more errors during the EE condition, we cannot rule out entirely that the reduced N400 amplitudes in the control group during this condition were associated with a difference in proficiency. Otherwise, given that no statistically significant differences were observed among the groups for the reaction times in the other conditions and that L2 proficiency was not differentiated, the differential EEG responses revealed during the GE and GG conditions would clearly suggest a training-related functional reorganisation. In line with this, we propose that the enhanced N400 responses in the SI group might reflect a training-related altered sensitivity to lexical–semantic processing within and across L1 and L2, probably relying on stronger connections within and between the lexicons. The results of the present study show that the differential N400 response patterns to incongruent noun pairs occur in the early processing stage of the N400 component (between 300 and 400 ms), this supporting the notion that these amplitude differences reflect differential time course of lexical–semantic access between the two groups.

An alternative explanation is that the enhanced N400 responses we revealed in the SI group were associated with more co-activated lexical–semantic neighbourhoods (i.e. number of semantically words simultaneously activated) in the mental lexicons (Midgley et al., 2009) because at least one previous study has shown that words from dense neighbourhoods elicit larger N400 responses than words from sparse neighbourhoods (Holcomb et al., 2002). Together with the findings of Holcomb et al., the present data may indicate that in SI group the semantic representations of L1 and L2 words are physiologically more richly interconnected, this leading in turn to a wider co-activation of lexical–semantic neighbourhoods.

3.5. Limitations

In the present study, we failed to uncover electrophysiological differences between the two groups in the specifically trained language direction (L2 to L1); this observation probably associated with the task used. SI are specifically trained to translate sentences and do not perform a literal translation of every individual word they hear, but instead semantically integrate the heard stream of speech into large scale windows. In a follow-up study, we will specifically examine auditory

sentence comprehension in SI and matched controls in order to clarify this issue.

4. Experimental procedures

4.1. Participants

Twenty-two native German subjects (9 women and 2 men per group) in the age range from 28 to 48 years (mean age 39±6 SD) participated in the present study. Specifically trained and certified graduated professional SI (SI training college) professionally interpreting only in one direction (backwards translation), namely from L2 (English) to L1 (German) were recruited. The controls were matched for age, gender, L2 proficiency and age of acquisition. Furthermore, all subjects have university degrees. Table 3 reports the biographical and behavioural data for each subject; Table 4 shows a comprehensive list of the foreign languages spoken by the subjects. No participant had a history of neurological, psychiatric or audiological disorders and all subjects were consistently right-handed according to the Annett-Handedness-Questionnaire (Annett, 1970). Subjects gave written consent in accordance with procedures approved by the local ethics committee (local ethic committee of the canton of Zürich, Switzerland) and were paid for their participation.

4.2. Procedure and stimuli

Subjects were seated in a dimmed and acoustically shielded room at about 110 cm distance from a monitor and were instructed to fixate on a small cross at the centre of the screen avoiding movements during data recording. Every subject performed 4 randomised runs (block design) of a semantic decision task within and across two languages: (1) English–English (EE), (2) German–German (GG), (3) English–German (EG) and (4) German–English (GE). During this semantic decision task, the subjects listened to semantically congruent and incongruent noun pairs within or across languages. The subjects were instructed to focus their attention on the auditorily presented noun pairs and to decide whether the two nouns were semantically congruent or incongruent by pressing a keyboard button; this task therefore implying the categorisation of semantic information. The reason for using auditory and not visual presented nouns was that SI are specifically trained to translate acoustic signals. Each run had a duration of 12 min and consisted of 67 semantically congruent (i.e. journey-travel/Fahrstuhl-Aufzug/Flasche-bottle/damage-Schaden) and incongruent (i.e. traffic-poison/Ampel-Rücken/König-surprise/flower-Hafen) noun pairs (www.neurowissenschaft.ch/mmeyer/Trans/). We adopted 536 word pairs in total. The EEG recording time was 48 min.

All auditory stimuli were recorded by a bilingual German–Canadian female speaker and further processed by means of the Adobe speech editing software (Adobe Audition 1.5). The stimuli were registered as 16 bit stereo files and matched for intensity (amplitude normalisation) by using the Adobe Audition software. The nouns were presented binaurally with a sound pressure level of about 50 Db (Digital Sound Level Meter 329, Voltcraft) using Hifi-headphones (Sennheiser, HD 25-1, 70 Ω, Ireland). The stimuli were matched for syllables length (disyllabic nouns), word frequency (www.corpora.uni-leipzig.de/) and double checked by a professional linguist for linguistic plausibility. The auditory stimuli had a mean duration of 800 ms, the inter-stimulus interval between both nouns of the pair was 1600 ms. In order to avoid response related artefacts, we inserted a delay period of 500 ms before the response selection. For the same reason, an inter-trial interval of 1200 ms after response selection was applied. So as to collect behavioural data, we required a response by pressing two keyboards buttons with the right fore and middle finger (congruent/incongruent). The presentation of the stimuli and recording of responses was controlled by the Presentation software (www.neurobs.com). All participants were native German speakers thus language proficiency (listening, grammar and vocabulary) was only tested in L2 (DIALANG software, www.dialang.org/german/index.htm). DIALANG allows the categorisation of language proficiency into 6 levels, namely A1, A2, B1, B2, C1 and C2 (ordered from low proficiency to good language skills). The particular advantage of this software is that it allows the testing of auditory sentence comprehension, a fundamental aspect for solving the semantic decision task we adopted. Language testing lasted about 40 min and was done the same day as the EEG measurement.

Table 4 – Acquisition of foreign languages.

Subjects	Languages
1	Spanish (24)
2	Italian (27)
3	French (12), Spanish (16), Italian (25)
4	French (12), Italian (22), Spanish (32)
5	French (20), Italian (22)
6	French (12), Spanish (21)
7	Spanish (20), Italian (22), Portuguese (41)
8	French (18), Italian (20)
9	French (6), Spanish (21), Serbian (25)
10	French (14), Italian (17), Swedish (32)
11	French (13), Spanish (15)
12	French (4), Italian (11)
13	French (17)
14	French (12), Italian (16)
15	French (13)
16	French (11), Tamil (16), Amharic (23)
17	French (10), Italian (16), Spanish (21), Indonesian (23)
18	Italian (19), Spanish (26)
19	French (12)
20	French (13), Italian (16), Spanish (24)
21	French (13), Spanish (23)
22	French (13)

The table reports the foreign languages spoken by the subjects and the age of acquisition. The first 11 subjects listed were SI.

4.3. EEG recording and analysis

EEG (59 electrodes+2 zygomatic eye channels, provided by Easy cap) was recorded with a sampling rate of 500 Hz and a band pass filter (0–100 Hz) using an EEG-amplifier (Brainproducts, Munich, Germany). The electrodes were located at frontal, temporal, parietal and occipital scalp sites according to the international 10–10 system (FP1, FP2, AF3, AF4, F7, F5, F3,

F1, Fz, F2, F4, F6, F8, FT7, FC5, FC3, FC1, FCZ, FC2, FC4, FC6, FT8, T7, C5, C3, C1, CZ, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPZ, CP2, CP4, CP6, TP8, TP10, P7, P5, P3, P1, PZ, P2, P4, P6, P8, PO7, PO3, POZ, PO4, PO8, O1, OZ, O2). We applied sintered silver/silver-chloride-electrodes (Ag/AgCl) and used the left Mastoid position (TP 9) as on-line reference. Electrode impedance was reduced to <10 kΩ by Electrogel conductant. We used Brain Vision Analyser software (Version 1.04, Brainproducts, Munich, Germany) for all steps of digital EEG raw data processing. EEG was continuously recorded and synchronised with the onset of every presented word.

The data were high- and low-pass filtered at 1–30 Hz. Artefacts were removed manually when possible or using an independent component analysis (ICA) (Jung et al., 2000). The processed data were re-referenced off-line to a linked-mastoid reference (Cummings et al., 2006; Moreno and Kutas, 2005) into 1100 ms segments. A baseline correction relative to the –100 to 0 ms pre-stimulus time period was applied. Epochs were averaged for each subject according to stimulus type and run. In addition, multi-subject grand averages were computed. A region of interest (ROI) over the posterior midline was defined for the evaluation of the N400 component because of the high similarity between neighbouring electrodes and in order to avoid multiple comparisons (Eichele et al., 2005). This ROI (CPz, Cz, Pz) was obtained by pooling the respective electrodes into one measure (Phillips et al., 2006). In order to evaluate N400 responses to congruent and incongruent nouns, we computed mean voltage magnitudes within multiple 50 ms windows in the time range from 300 to 700 ms, namely 300–350, 350–400, 400–450, 450–500, 500–550, 550–600, 600–650 and 650–700 ms (Phillips et al., 2006). In this study, we explicitly chose not to calculate the N400 effect (incongruent minus congruent) and evaluated the electrophysiological responses to congruent/incongruent trials separately. The reason for this is that professional SI always interpret in a meaningful context and are not specifically trained for processing incongruence. Consequently, we explicitly distinguished between the processing mode of congruent and incongruent trials. The electrophysiological responses to the first noun in the pair were not evaluated because they were not of interest for the present study.

Acknowledgments

During the preparation of this manuscript, SE, LJ and MM were supported by Schweizer National Fonds (Swiss National Foundation) SNF grant 320000-120661/1. We would like to express our gratitude to Manuela Beretta-Vrontzos and Christine Lüthy for EEG measurements. Furthermore we are grateful to Dorothea Weniger for the inspiring discussions about this study.

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3.2. Study B: Differential Language Expertise Related to White Matter Architecture in Regions Subserving Sensory-Motor Coupling, Articulation, and Interhemispheric Transfer.

Full Citation:

Elmer, S., Hänggi, J., Meyer, M., and Jäncke, L. Differential language expertise related to white matter architecture in regions subserving sensory-motor coupling, articulation, and interhemispheric transfer. *Human Brain Mapping* 32: 2064-2074, 2011.

3.2.1. Abstract

The technique of diffusion tensor imaging (DTI) has been used to investigate alterations in white matter architecture following long-term training and expertise. Professional simultaneous interpreters (SI) provide an ideal model for the investigation of training-induced plasticity due to the high demands placed on sound to motor mapping mechanisms, which are vital for executing fast interpretations. In line with our hypothesis, we found clusters with decreased fractional anisotropy (FA) in the SIs group in brain regions previously shown to support sensory-motor coupling mechanisms and speech articulation (cluster extent family-wise error corrected, $P < 0.01$). Furthermore, we found an altered white matter architecture indicated by lower FA values in the SIs group in the most anterior and posterior parts of the corpus callosum. Our results suggest that language expertise is accompanied by plastic adaptations in regions strongly involved in motor aspects of speech and in interhemispheric information transfer. These results have implications for our understanding of language expertise in relation to white matter adaptations.

◆ Human Brain Mapping 32:2064–2074 (2011) ◆

Differential Language Expertise Related to White Matter Architecture in Regions Subserving Sensory-Motor Coupling, Articulation, and Interhemispheric Transfer

Stefan Elmer*, Jürgen Hänggi, Martin Meyer, and Lutz Jäncke

Division Neuropsychology, Institute of Psychology, University of Zurich, Zurich, Switzerland

Abstract: The technique of diffusion tensor imaging (DTI) has been used to investigate alterations in white matter architecture following long-term training and expertise. Professional simultaneous interpreters (SI) provide an ideal model for the investigation of training-induced plasticity due to the high demands placed on sound to motor mapping mechanisms, which are vital for executing fast interpretations. In line with our hypothesis, we found clusters with decreased fractional anisotropy (FA) in the SI group in brain regions previously shown to support sensory-motor coupling mechanisms and speech articulation (cluster extent family-wise error corrected, $P < 0.01$). Furthermore, we found an altered white matter architecture indicated by lower FA values in the SI group in the most anterior and posterior parts of the corpus callosum. Our results suggest that language expertise is accompanied by plastic adaptations in regions strongly involved in motor aspects of speech and in interhemispheric information transfer. These results have implications for our understanding of language expertise in relation to white matter adaptations. *Hum Brain Mapp 32:2064–2074, 2011.* © 2010 Wiley Periodicals, Inc.

Key words: diffusion tensor imaging; plasticity; multilingualism; insula; corpus callosum; simultaneous interpreters

INTRODUCTION

Several recent longitudinal [Draganski et al., 2004; Hyde et al., 2009] and cross-sectional [Maguire et al., 2000] studies have described the exceptional potential of the human brain to alter its function and morphology following short- and long-term training or exposure to specific environments. As many as 10 studies investigating plastic adaptations in professional musicians have clearly demonstrated white matter reorganization after intensive instrumental training that required the integration of sensory and motor information [Bengtsson et al., 2005; Imfeld et al., 2009]. Similar adaptations in the white matter architecture have also been observed in other domains, for instance, in individuals undergoing intensive motor training that places high demands on sensory-motor coordination [Jäncke et al., 2009; Hänggi et al., 2009; Baumann et al., 2007; Jäncke 2009; Jäncke et al., 2000; Münte et al., 2002].

An established dual stream model [Hickok and Poeppel, 2007] suggests that anatomically and functionally segregated pathways are involved in different aspects of language processing. This model postulates that a bilateral ventral processing stream originating from posterior perisylvian sites and stretching to anterior temporal regions

Contract grant sponsor: Swiss National Science Foundation (SNF); Contract grant number: 320030-120661 to M.M..

Stefan Elmer and Jürgen Hänggi contributed equally to this study.

*Correspondence to: Stefan Elmer, Dr.des., Division Neuropsychology, Institute of Psychology, University of Zurich, Binzmühlestrasse 14/25, CH-8050 Zurich, Switzerland. §Stefan Elmer and Jürgen Hänggi contributed equally to this study.
E-mail: s.elmer@psychologie.uzh.ch

Received for publication 11 February 2010; Revised 2 August 2010; Accepted 27 August 2010

DOI: 10.1002/hbm.21169

Published online 15 December 2010 in Wiley Online Library (wileyonlinelibrary.com).

supports a variety of language comprehension functions, implying that this ventral stream is strongly involved in mapping sound to meaning. On the other hand, a left dorsal stream that extends from posterior perisylvian regions to the frontal operculum is proposed to be involved in auditory-to-motor transformations and in articulation processes, and thus important for mapping sounds to articulation. A previous study [Saur et al., 2008] investigated the neuronal substrate of the dual stream model by combining functional magnetic resonance imaging (fMRI) during performance of two prototypical language tasks with diffusion tensor imaging-based (DTI) tractography techniques. These two tasks, sublexical repetition and higher-level language comprehension, were designed to differentially recruit the dorsal and ventral processing streams. The results of this study corroborated the integrity of the model proposed by Hickok and Poeppel [2007] and pointed to a functional and anatomical segregation of the two processing streams.

In speech production, the left inferior frontal gyrus and particularly Broca's area were long thought to be critical for the motor act of speech [Ruff and Arbit, 1981; Schiff et al., 1983]. However, lesion-based analyses conducted with large samples [Bates et al., 2003; Dronkers, 1996] have shown that the integrity of the left anterior insula and not necessarily Broca's area is fundamental for accurate articulation. The functional relevance of the left insula for speech articulation is further supported by a positron emission tomography (PET) study conducted by Wise et al. [1999]. These authors showed that the repetition of single words did not activate just Broca's area but a more comprehensive motor-related network including the left anterior insula, the lateral premotor cortex, and the basal ganglia. Wise and colleagues were further able to establish that the left anterior insula is activated during both hearing and articulation, thus supporting the notion that this region plays a pivotal role in sensory-motor coupling mechanisms in language. Such a sensory-motor interplay supported by the anterior insula was previously been shown to be restricted to overt task performances [Riecker et al., 2000].

Several neuroimaging studies of overt speech production [Eickhoff et al., 2009] and observations in patients with specific language impairments such as verbal apraxia [Dronkers, 1996] have revealed a broad network that contributes to the control of speech motor output. A previous meta-analysis [Eickhoff et al., 2009] of neuroimaging data acquired in healthy subjects during verbal fluency tasks identified the involvement of a core motor network in overt speech production. This network is composed by the pars opercularis, left anterior insula, basal ganglia, cerebellum, premotor cortex, and primary motor cortex. Further evidence for structures mediating speech production has been derived from the analysis of patients with specific clinical syndromes [Nestor et al., 2003] and developmental language disorders [Jüncke et al., 2007]. Nestor et al. used the PET technique to investigate 10 patients affected by progressive nonfluent aphasia, a syndrome in which the patient loses the ability to communicate fluently [2003]. Compared with controls and with a group of Alzheimer's disease patients without nonfluent aphasic features, the nonfluent aphasia group showed hypometabolic activation patterns most notably in the left anterior insula/frontal opercular region. This clinical finding underscores the crucial role of this structure in motor aspects of speech.

The functional relevance of the white matter fiber bundles in speech production has been investigated in individuals diagnosed with specific speech disorders such as persistent developmental stuttering. A previous voxel-based morphometry (VBM) study [Jäncke et al., 2004] found enhanced stuttering-related white matter volumes in regions supporting speech production functions, including the white matter underlying the pars triangularis and the precentral gyrus in the vicinity of the face and mouth representation. Another VBM study [Beal et al., 2007] delivered further evidence in favor of the notion that stuttering is related to differential white matter architecture in regions involved in speech production. That study reported lower white matter densities in affected individuals in a region enclosing the left anterior insula.

The DTI technique can be especially useful for understanding the role of brain connectivity in human behavior, since the white matter bundles support the crosstalk between grey-matter areas that enables them to function in concert. In the domain of speech processing, SI represent an ideal experimental group for studying the architecture of white matter fiber bundles in conjunction with language expertise and plastic adaptations [Elmer et al., 2010]. Professional simultaneous interpreting places high demands on sensory-motor coupling mechanisms; since linguistic input needs to be almost simultaneously translated into an adequate output format. Furthermore, the intensive training of SI requires fine-tuned sensory-motor adjustments in order to achieve an excellent pronunciation in the foreign languages.

In this study, we used a voxel-wise approach to compare fractional anisotropy (FA) in SI and control subjects. We focussed on the white matter architecture in brain regions previously shown to be involved in mapping sounds to articulation and in the motor control of speech. We expected that the fast sound-to-motor mapping typical for simultaneous interpreting must be accompanied by plastic adaptations in white-matter pathways situated along the dorsal stream, in keeping with the model proposed by Hickok and Poeppel [2007]. In particular, we expected to find FA differences between the two groups in white-matter fibers that encompass the left anterior insula, the Broca's area, the basal ganglia, the left ventral prefrontal region, and the motor/premotor areas.

MATERIALS AND METHODS

Participants

We investigated 24 healthy right-handed subjects divided into two groups of 12 subjects each. The

experimental group (SI, eight women and four men, mean/standard deviation: 37.9 ± 5.8 years) was compared with a control group (eight women and four men, 28.4 ± 2.8 years). The SI group consisted of specifically trained and certified graduated professional SI. Since all participants had a comparable level of education (i.e., university degree or advanced university students), we exclude that different IQ values between the two groups may influence the results in some directions. Additionally, the regions that we observed to differ between groups have not yet been attributed to IQ [Chiang et al., 2009; Jung and Haier, 2007; Li et al., 2009]. The subjects reported no past or current neurological, psychiatric, or neuropsychological problems and denied to take drugs or illegal medication. Subjects were paid for participation. The local ethics committee (Zürich, Switzerland) approved the study and written informed consent was obtained from all participants.

Imaging Data Acquisition

Magnetic resonance imaging (MRI) scans were acquired on a 3.0 T Philips Achieva whole body scanner (Philips Medical Systems, Best, The Netherlands) equipped with a transmit-receive body coil and a commercial eight-element sensitivity encoding (SENSE) head coil array.

A diffusion-weighted spin echo, echo-planar imaging (EPI) sequence was used to obtain diffusion-weighted scans with a measured spatial resolution of 2.08 × 2.08 × 2.0 mm (acquisition matrix 96 × 96 pixels, 50 slices) and a reconstructed resolution of 1.56 × 1.56 × 2.0 mm (reconstructed matrix 128 × 128 pixels, 50 slices). Further imaging parameters were as follows: Field of view, FOV = 200 × 200 mm; echo time, TE = 50 ms; repetition time, TR = 10,166 ms; flip angle, FA = 90°; sensitivity encoding (SENSE) factor, R = 2.1; and b-value = 1,000 s/mm^2. Diffusion was measured in 15 noncollinear directions followed by a nondiffusion-weighted volume (reference volume). We used the Philips standard diffusion gradient mode ("medium") that is comprised by 16 diffusion directions (15 noncollinear diffusion directions and one nondiffusion weighted volume). We did not acquire a b0-field map for correcting EPI-distortions because we used the sensitivity encoding (SENSE) technique that minimizes these EPI-distortions typically occurring at the base of the brain and in medial prefrontal regions. All these areas were not expected to be altered in SI. Total acquisition time was about 15 min.

Analysis of Fractional Anisotropy and Axial Versus Radial Diffusivity

To analyze interconnectivity, measured by means of fractional anisotropy (FA), we preprocessed the diffusion-weighted images with the scripts of tract-based spatial statistics (TBSS) [Behrens et al., 2003] and the diffusion toolbox (FDT). This toolbox is part of the FSL [Smith et al., 2006] software implemented in the functional magnetic resonance imaging of the brain (FMRIB) software library (http://www.fmrib.ox.ac.uk/fsl/) and was used to create FA as well as axial (AD) and radial diffusivity (RD) maps. The following steps were realized: (1) Head movement and eddy current correction was applied using EDDY_CORRECT of FDT. (2) A brain mask of the reference volume (no diffusion) was created using the brain extraction tool (BET). (3) Tensors were fitted to the data using DTIFIT to generated FA, AD, and RD maps. (4) Nonlinear registration of all FA, AD, and RD maps into standard space was applied. (5) FA maps were smoothed with a Gaussian kernel of full width at half maximum (FWHM) of 9 mm. (6) All voxels with FA values smaller than 10% of the mean FA values were excluded from the statistical analyses because we were only interested in the diffusion characteristics of white matter tissue. We additionally regressed the age of the participants against local FA values in order to control for age differences between the interpreters and the control subjects. AD and RD was computed only for the clusters that showed a significant difference in FA.

Statistical Analysis

The statistical group comparisons of local FA as well as the regression with age were performed by applying the general linear model implemented in the statistical parametric mapping (SPM5) software (http://www.fil.ion.ucl.ac.uk/spm/). Global mean FA was modeled as a nuisance variable in the analysis of covariance of local FA as well as in the regressions applied for controlling the variable age. Although strong a-priori hypotheses were postulated, the statistical extent threshold was corrected for multiple comparisons combined with a nonstationary smoothness correction [Hayasaka and Nichols, 2004; Hayasaka et al., 2004]. We used cluster extent family-wise error (FWE) correction with $P = 0.01$ and a height threshold of $P = 0.001$ (uncorrected) for FA group comparisons and the regression with age. Note that the number of voxels that were found to be different in the whole brain FA analysis and those used to compute AD and RD slightly differs. This is due to the nonstationary smoothness correction applied in the FA analysis. This correction cannot be applied to the region-of-interest approach used to compute AD and RD.

RESULTS

Fractional Anisotropy and Axial Versus Radial Diffusivity

In this study, fractional anisotropy (FA) maps in SI (n = 12) and control subjects (n = 12) were compared using a voxel-wise approach to examine the directedness and integrity of the white matter architecture in brain regions previously shown to be involved in the mapping sounds to articulation, in the motor control of speech, as well as in the interhemispheric transfer.

TABLE I. Results of the FA analysis (controls > interpreters)

Fractional anisotropy	Hemisphere	MNI coordinates			Cluster size	*t*-value
Controls > Interpreters		*x*	*y*	*z*	$k = 1{,}359$ voxels nonstationarity corrected	$P < 0.01$ (FWE) cluster extent corrected
Orbitofrontal cortex	Right	18	30	−15	1,635	6.82
Genu of corpus callosum	Right	21	30	−3		3.91
Insula	Left	−26	23	12	1,546	6.49
Splenium of corpus callosum	Left	−5	−44	20	3,226	6.46
Splenium of corpus callosum	Left	−21	−57	18		5.04
Body of corpus callosum	Left	−13	−39	19		5.82
Cingulum	Left	−3	−24	30	2,228	6.11
Corticospinal tract	Left	−22	−3	38		6.05
Cingulum	Left	−10	−27	38		5.07
Inferior parietal lobe	Right	45	−76	29	1,372	6.08
Inferior parietal lobe	Right	51	−57	35		4.38
Forceps minor	Left	−17	48	2	2,219	5.94
Forceps minor	Left	−14	57	9		5.38
Frontal pole	Left	−21	56	1		4.15
Nucleus caudatus	Right	11	7	19	4,968	5.92
Forceps minor corpus callosum	Right	1	31	9		5.18
Genu of corpus callosum	Left	−5	25	5		5.13

In line with our hypothesis, subjecting the contrast controls versus SI to the voxel-wise analysis of FA values, we revealed strong between-group differences (Table 1 and Figure 1) in fiber tracts encompassing the left anterior insula (peak in Montreal Neurological Institute coordinates: $x = -26$, $y = 23$, $z = 12$; $t = 6.49$), the upper part of the corticospinal tract (peak: $x = -22$, $y = -3$, $z = 38$; $t = 6.05$), the right inferior parietal lobe (peak: $x = 45$, $y = -76$, $z = 29$; $t = 6.08$ and peak: $x = 51$, $y = -57$, $z = 35$; $t = 4.38$), and the dorsal part of the right caudate nucleus (peak: $x = 11$, $y = 7$, $z = 19$; $t = 5.92$).

As a second main result, we found lower FA values in the SI group in the genu (peak: $x = 21$, $y = 30$, $z = -3$; $t =$

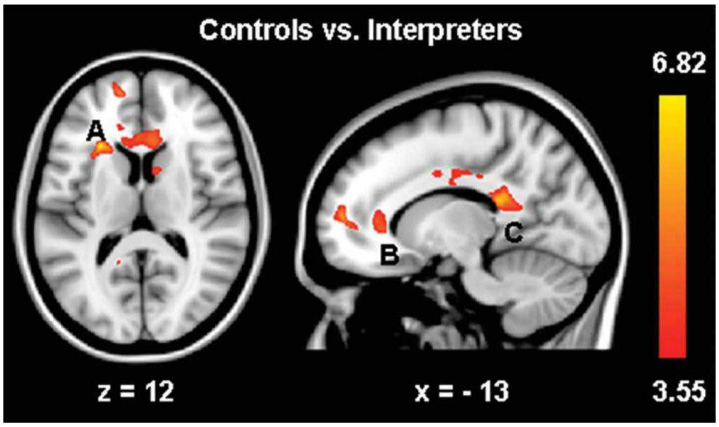

Figure 1.

FA, controls versus SI. Statistical parametric maps of the voxel-based fractional anisotropy analysis overlaid on the MNI-152 template and thresholded with $P < 0.01$, FWE-corrected at the cluster extent level. Shown are regions with increased fractional anisotropy in the control subjects compared with simultaneous interpreters in the left insula (A, left image), in the genu (B, left and right image), and in the body and splenium (C) of the corpus callosum (right image).The color bar represents the *t*-values.

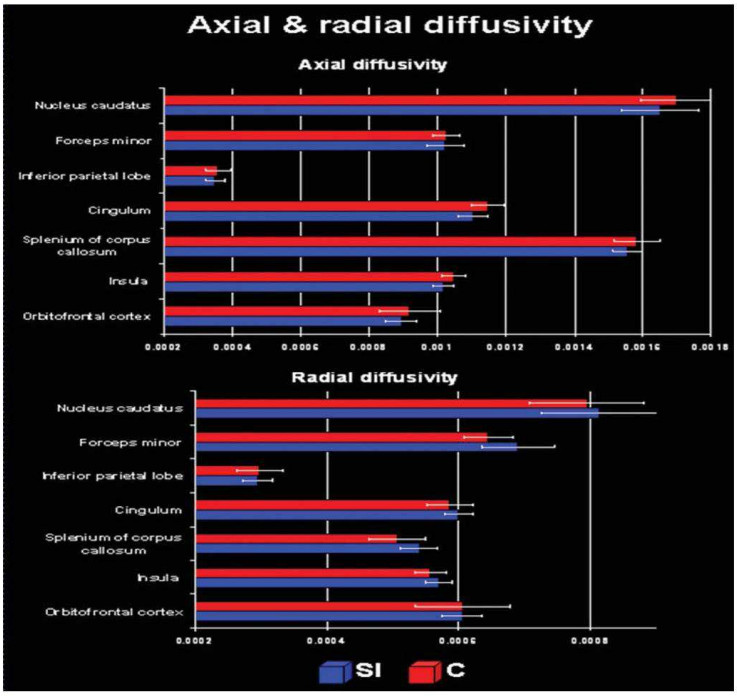

Figure 2.
Average mean diffusivity (mm^2/s). The figure depicts average axial and radial diffusivity for each significant cluster and group.

3.91 and peak: $x = -5$, $y = 25$, $z = 5$; $t = 5.13$) and splenium (peak: $x = -5$, $y = -44$, $z = 20$; $t = 6.46$ and peak: $x = -21$, $y = -57$, $z = 18$; $t = 5.04$) of the corpus callosum. Furthermore, we revealed lower FA values in the SI group in the body of the corpus callosum (peak: $x = -13$, $y = -39$, $z = 19$; $t = 5.82$). No brain area was found to have higher FA values for the opposite contrast (SI vs. controls). A comprehensive list of all results is depicted in Table I.

To better comprehend the decrease in FA values for the highly trained subjects, we calculated the average axial and radial diffusivity (mm^2/s) for each significant cluster and group. As visible in Figure 2, our DTI data show that the lower FA values in the interpreters group are associated with reduced axial and enhanced radial diffusivity.

Regression With Age

Since the two groups significantly differed in age (*t*-test for independent samples, two-tailed, controls vs. SI, $t(df = 22) = -4.71$, $P < 0.001$), we computed a regression of FA values with age. This analysis yielded a positive correlation between FA and age in the white matter residing in the orbitofrontal cortex (peak: $x = 7$, $y = 48$, $z = -15$; $t = 6.81$ and peak: $x = 4$, $y = 45$, $z = -25$; $t = 5.34$ and peak: $x = -3$, $y = 37$, $z = -23$; $t = 4.21$).

DISCUSSION

General Discussion

The motivation of this study was based on the hypothesis that the fast sound-to-motor transformations necessary for simultaneous interpreting must be accompanied by plastic adaptations in white matter pathways stretching along the left dorsal language stream according to the model proposed by Hickok and Poeppel [2007] and supported by previous studies concerning overt speech production [Eickhoff et al., 2009] or speech disorders [Dronkers, 1996]. With this background in mind, we tested for white matter differences between SI and matched controls by comparing FA values derived from the DTI data and report two principal findings (Fig. 1 and Table I). The

first main result was that we found substantial between-group differences in white matter architecture as indicated by reduced FA in the SI group in regions involved in the control of speech articulation and sensory-motor coupling mechanisms. These areas are the left anterior insula, the basal ganglia, the inferior parietal lobe, and the upper part of the corticospinal tract. The second main result was the finding of reduced FA values in the SI group in the anterior (genu), middle (body), and posterior (splenium) part of the corpus callosum, a large fiber bundle in the human brain that predominantly interconnects homologous cortical areas of both hemispheres [Nolte, 1999]. Our results thus suggest differential white matter architecture in regions supporting speech articulation, sensory-motor coupling mechanisms, and interhemispheric callosal transfer. We propose that these expertise-related morphological adaptations are due to specific language-related demands associated with simultaneous interpreting.

Fractional Anisotropy and White Matter Plasticity

Our results are comparable with previous work showing that intensive musical training [Imfeld et al., 2009] or fine tuned motor praxis [Hänggi et al., 2009; Jäncke et al., 2009] abets plastic adaptations associated with decreased FA values. Partly in contrast to our findings, a former neuroanatomical study investigating professional pianists using the DTI technique revealed increased FA values with increasing amount of practice hours in this group [Bengtsson et al., 2005]. Although this correlation suggests that increased practice might lead to increased FA, the mean FA values were mostly smaller in pianists compared with nonpianists (see Table I in Bengtsson et al., 2005]. Thus, overall the experts (here the pianists) demonstrate generally lower FA values in many fiber tracts compared with nonexperts.

To date, it results difficult to fundamentally explain the findings arising from FA and diffusivity measurements and associate them with the knowledge deriving from cellular neurophysiology. On the basis of a previous work conducted by Mori and Zhang [2006], we know that there are at least three possibilities that lead to lower FA: (1) an increase in radial diffusivity (along the shorter axes); (2) a decrease in axial diffusivity (along the longest axis); (3) the combination of the two. In addition, crossing fibers lead to decreased FA values at the intersections. On the other hand, a meticulous technical review [Beaulieu, 2002] of the DTI technique evidences that the interpretation of water molecules diffusion is much more complex as previously supposed. Beaulieu provides empirical evidence for the fact that the available data do not permit the dissection of the individual contributions of myelin and axonal membranes to the degree of anisotropy. However, empirical evidence suggests that axonal membranes play the primary role and that myelination, although not necessary for significant anisotropy, can modulate the degree of anisotropy. This implicates further reasoning to explain how training-induced neuronal adaptation can lead to lower FA values.

As visible in Figure 2 our DTI data militate in favor of the view that the lower FA values in the interpreters' group are associated with reduced axial and enhanced radial diffusivity. For example, it might be that the specific stimulation and usage of the language and sensory-motor control systems might have resulted in a more complex architecture of the fiber bundles in the form of less parallel devolution. A further possibility might be that increased myelin sheaths may reduce the volume of the extracellular space and simultaneously increase the intracellular radial diffusivity relative to its extracellular counterpart; this leading to lower FA values. To further clarify which of these aforementioned mechanisms (or even others) are responsible for the changes in FA reported here, it is necessary to conduct further methodological research.

Sensory-Motor Coupling and Speech Articulation

The insula has a varying cytoarchitectonic arrangement throughout its length and subserves a plethora of different functions: visceral, motor, vestibular, somatosensory, and auditory functions [Flynn et al., 1999]. However, the anterior part of the insula, in the proximity of the extreme capsule, has been shown to have connections to the brain stem and to the pontine nuclei [Ozaki et al., 1986]. The latter serve as a relay station for corticopontine fibers that carry information from the primary motor cortex and have projections to the cerebellum via the middle cerebellar peduncle. The direct and indirect anatomical connections of the anterior insula with several motor structures suggest that this region is strongly involved in fine tuned motor adjustments and modification of actions. In addition, the anterior insula is known to have connections to the supratemporal plane [Flynn et al., 1999] and to the caudate nucleus [Turner et al., 2009]. These direct or indirect crosslinks between the anterior insula with several motor structures and its connections to the supratemporal plane support the notion that this region subserves speech articulation and sounds to motor mapping functions. In fact, previous neuroimaging [Ackermann and Riecker, 2004; Riecker et al., 2000; Wise et al., 1999] and lesion studies [Bates et al., 2003; Dronkers, 1996] have demonstrated that the left anterior insula is generally involved in the coordination of motor aspects of speech [Riecker et al., 2000; Wise et al., 1999], of muscles engaged in articulation and phonation [Ackermann and Riecker, 2004] and involved in the motor planning of speech, as shown in patients with apraxia of speech [Dronkers, 1996]. In view of the differential white matter architecture we found between the two groups in the left anterior insula, the caudate nucleus, and in the upper part of the corticospinal tract, our results suggest an expertise-related structural adaptation in fiber bundles supporting speech articulation and sensory-motor coupling

mechanisms. In line with our hypothesis, we suggest that this expertise-related adaptation facilitates a more efficient neural processing during sound-to-motor mapping, which is a fundamental prerequisite for the simultaneous translation from an input language to a target language.

The participation of the left anterior insula in sounds-motor associations was previously corroborated in music-naïve individuals undergoing a short-term musical training [Mutschler et al., 2007]. Mutschler et al. investigated subjects who passively listened to simple piano melodies that had been either actively learned beforehand or simply listened to passively and found increased fMRI responses to actively compared with passively learned melodies in a region similar to that we found in this study. These previous results show that the left anterior insula becomes involved in sensory-motor coupling processes already after a short period of learning and may therefore play a role in learning and supporting sensory-motor associations. These results further suggest that the left anterior insula is involved in auditory-motor integration such as when sounds become meaningful to the motor system, probably reflecting a general auditory-motor interface.

In a meta-analysis of previously published neuroimaging data reporting insula effects, Mutschler et al. [2009] found language tasks and perception of vocalization to preferentially activate an area in the dorsal part of the left anterior insular cortex, thus suggesting that this subregion may be involved in general language functions. While we are fully aware of the anterior insula's involvement in a variety of heterogeneous functions, we are concerned here only with its role in language processing. The contribution of the left anterior insula to language processing is further supported by the results of a previous published voxel-based-morphometry (VBM) study [Golestani and Pallier, 2007]. This particular study revealed that individuals who more accurately learned to pronounce a Persian consonant that does not exist in French but which could easily be distinguished from French speech sounds had higher white matter densities in the white matter enclosing left anterior insula. Interestingly, the differential cluster we found in the anterior insula ($x = -26$, $y = 23$, $z = 12$) has almost the same anatomical location as reported by Golestani and Pallier ($x = -29$, $y = 29$, $z = 10$) in fast foreign speech learners. This is not surprising, since SI can be considered as individuals able to learning foreign languages with high proficiency. Foreign speech learning places a high demand on sensory-motor coupling mechanisms, since the pronounced sound continuously undergoes fine tuned sensory-motor adjustments in order to achieve an excellent pronunciation in the foreign language. We thus propose that the ability to rapidly regulate sound-to-motor transformations may be a basic prerequisite for enrolment in simultaneous interpreting college. However, an additional intensive training in this specific domain is necessary to become a certified and graduated professional SI. This hypothesis could be the starting point for developing a sensitive test for separating suitable training candidates, since selection during education is known to be time consuming and costly.

Meanwhile, it is established that the left anterior insular region is phylogenetically ancient and belongs to the archicortex. Even if this region evolved relatively early in evolution, there is evidence in favor of the view that this brain region plays an important role in audio-motor integration [Mutschler et al., 2009] and in particular in the coordination of the up to 100 muscles engaged in articulation and phonation [Ackermann and Riecker, 2004, 2010]. Conceivably, the functional involvement of the left anterior insular region in speech production might have evolved within the framework of phylogenetically older connections between the insula and limbic structures. Otherwise, it is imaginable that the contribution of the left anterior insula to speech production was established through connections between this structure and nonspeech functions of the upper midline musculature in association with swallowing [Ackermann and Riecker, 2004].

Callosal Transfer

Genu of the corpus callosum

The anatomy of the corpus callosum has been proposed to be a potential marker for functional lateralization because its size is considered proportional to the number of fibers connecting the two hemispheres [Josse et al., 2008]. In line with this, a previous morphometric study [Schlaug et al., 1995] showed that professional musicians who began musical training before the age of 7 revealed a larger mid-sagittal area in the anterior part of the corpus callosum than did control subjects, indicating a training-induced difference in interhemispheric communication between sensory-motor areas.

The anterior part of the corpus callosum contains fiber tracts connecting frontal and orbitofrontal areas of both hemispheres [Huang et al., 2005]. Many of these fibers are involved in the control of motor and somatosensory functions. However, other fibers support the interhemispheric communication between both insulae and prefrontal areas [Delacoste et al., 1985; Dimond et al., 1977]. It is now established that prefrontal regions play an essential role in the integration of information and the management of multiple tasks [Reynolds et al., 2006] and are thus crucial in subserving higher cognitive functions such as memory, attention, and inhibition. Indeed, all these cognitive functions are strongly involved in simultaneous interpreting. In line with this, the differential architecture we revealed in the genu of the corpus callosum suggests that professional interpreting is accompanied by plastic adaptations in a structure that facilitates executive control mechanisms. In particular, the morphological differences we found in the genu of the corpus callosum suggest that simultaneous interpreting may have an influence on the transfer time of information across multiple frontal areas for enhancing executive control.

One particular PET study [Rinne et al., 2000] measured brain activation in professional interpreters during simultaneous interpreting versus repetition of auditorily presented sentences, reporting clear evidence of the high demands placed on executive control during interpreting. The relevance of prefrontal regions for language translation is further supported by another PET study [Klein et al., 1995] designed to investigate translation compared with the repetition of single auditorily presented words in English-French bilinguals. Similar prefrontal activations were also found in a language-switching fMRI study [Hernandez et al., 2000], which investigated single- and dual-language picture naming in a group of Spanish-English bilinguals. Interestingly, a comparable involvement of prefrontal areas was also reported in several switching tasks that were not principally related to language processing [Yeung et al., 2006]. All these findings are congruent with the view that language switching, a fundamental prerequisite for translation, is part of a general executive attentional system residing in the prefrontal cortex [Hernandez et al., 2000]. Hence, we suggest that the differential architecture in the genu of the corpus callosum may support efficient control of switching-related mechanisms by keeping one language from interfering with the other during speech. Our results are also consistent with a previous morphometric study [Coggins et al., 2004] that evaluated the area of five subregions of the mid-sagittal corpus callosum in bilingual compared with monolingual individuals. The authors proposed that the measured adaptation in the anterior mid-body occurred in tracts connecting prefrontal regions, mainly to accommodate multiple language capacities and increase processing speed between the frontal lobes; this being advantageous in compensating for the processing load of maintaining multiple languages.

Splenium of the corpus callosum

The fibers connecting the temporal and parietal language-related regions of the two hemispheres cross the caudal part of the corpus callosum [Delacoste et al., 1985; Waddington, 1984]. Although language processing is the result of the coordination of activity between both hemispheres via the cerebral commissures [Coggins et al., 2004], it is known that the processing of speech sounds relies on important computational differences between the two hemispheres [Hickok and Poeppel, 2007]. The left auditory-related cortex is more proficient at processing stimuli requiring high-temporal resolution (segmental information), whereas the right counterpart is more responsive to processing spectral information (suprasegmental information) [Zatorre and Belin, 2001].

Although speech processing relies on fast changing signals more strongly involving the left auditory-related cortex [Zaehle et al., 2004], the prosody of speech is preferentially processed in the right auditory-related cortex [Meyer et al., 2002]. Professional interpreters rely on both segmental and suprasegmental information for performing an adequate translation, especially taking into account the huge variability of the speakers, their cultural background, the numerous languages spoken, and the informational relevance mediated by speech prosody. In this context, a previous EEG study [Friederici et al., 2007] has shown the functional relevance of the posterior third of the corpus callosum for the dynamic interplay of right and left auditory-related areas in patients with posterior callosal lesions. These results in combination with what is known about the functional anatomy of the corpus callosum lead to the suggestion that the FA differences we found in the splenium are the result of training-induced adaptations in interhemispheric connectivity between temporal and temporo-parietal auditory-related brain regions and that this is of relevance for a fine-tuned interplay between perisylvian regions.

A previous study on language expertise [Golestani et al., 2002] did show a relationship between white matter architecture and non-native speech sound learning. This study demonstrated that the speed of sound learning is correlated with FA in parieto-occipital regions and parts of the splenium of the corpus callosum. These anatomical differences are thought to be related to the more efficient neuronal processing in faster non-native speech sounds learners, this possibly due to greater interhemispheric connectivity in temporal and temporo-parietal auditory-related brain regions in fast phonetic learners. In a similar way, we suggest that the reduced FA we uncovered in the posterior part of the corpus callosum may be related to a higher or smaller degree of functional asymmetry in speech-related functions of temporo-parietal regions. Since several neuroimaging studies have repeatedly shown leftward asymmetries during tasks requiring phonetic processing [Demonet et al., 1992; Zatorre et al., 1992] and verbal working memory functions [Paulesu et al., 1993], we propose that the reduced FA we revealed in the splenium could be related to a more asymmetrical/symmetrical representation of phonetic perception or verbal working memory functions, these being essential for interpreting.

Differential White Matter Architecture in the Right Hemisphere

Our findings of differential white matter architecture deserve a particular consideration in the right hemisphere. In particular, we discuss the lower FA values we found in the SI group in the dorsal part of the right caudate nucleus and the right inferior parietal lobe in turn.

Caudate Nucleus

Meanwhile, there is mounting evidence supporting the notion that not only the left but also the right caudate nucleus is strongly involved in speech production [Abutalebi et al., 2008; Liu et al., 2010]. Furthermore, the participation of the right caudate nucleus in overt speech processing

was previously found in bilingual subjects during both language switching [Abutalebi et al., 2008; Price et al., 1999] and translation tasks [Abutalebi et al., 2007; Price et al., 1999]. In the context of bilingualism, previous researches [Abutalebi and Green, 2007; Abutalebi et al., 2008] have also associated the functional contribution of this anatomical structure with inhibition mechanisms, because during speech production one language has to be inhibited in order to avoid interferences between the two languages. Taken together, these previous observations speak in favor of the view that the right caudate nucleus may not only be related to articulo-motor processing but also to general brain mechanisms such as switching and inhibition mechanisms. Even though we are fully aware that bilingual subjects cannot be directly contrasted with the exceptional faculties observed in professional SI due to the intensive training demands, simultaneous interpreting strongly involves switching and inhibition. However, in the context of the findings of this work, it results difficult to allocate a univocal functional contribution on this anatomical structure, since this study only placed emphasis on anatomy without integration of behavioral aspects.

Inferior Parietal Lobe

Our present data agree with several recent neuroimaging and morphometric studies that sketched a bilateral cerebral implementation of language processing. In fact, right hemisphere structures were previously shown to play a prominent role in both speech production [Abutalebi et al., 2008; Golestani and Pallier, 2007; Golestani et al., 2002; Liu et al., 2010] and speech perception [Meyer et al., 2004; Schmidt et al., 2008]. Furthermore, previous findings argue in favor of the view that the right inferior parietal lobe is implicated in the storage of phonological information in verbal short-term memory [Jonides et al., 1998; Paulesu et al., 1993].

Meanwhile, there is willingness to consider the functional and morphologic characteristics of the right inferior parietal lobe as a likely neuroanatomical substrate subserving different aspects of language processing in association with training and expertise [Golestani and Pallier, 2007; Price et al., 1999]. Along this vein, the view of a right inferior parietal contribution to language expertise is consistent with a previous research conducted with German-English bilinguals who were scanned whilst either translating or reading visually presented words in German (L1), English (L2), or switching between L1 and L2 [Price et al., 1999]. The fact that switching between L1 and L2 (in both directions) was associated with increased bilateral activation of the inferior parietal lobe may indicate that switching modulates word processing at a phonological stage. Furthermore, a right inferior parietal contribution to phonemic processing is supported by a previous study [Zatorre et al., 1996], which showed that this region was stronger involved in phonemic detection than in nonverbal pitch detection. On the basis of this previous evidence for phonological processing in inferior parietal regions, we propose that professional interpreting may favor brain connectivity in regions associated with the storage of phonological information in verbal short-term memory. Otherwise, right hemispheric language processing was previously associated with the perception of auditory suprasegmental cues [Geiser et al., 2008; Meyer et al., 2002] that may help facilitate professional interpreting. These previous observations in compliance with our present data partially agree with the notion that language skills and expertise are associated with a right inferior parietal implementation of language processing.

CONCLUSIONS

In the present DTI study, we compared FA between SI and control subjects and expected to find differential white matter properties in regions supporting sensory-motor coupling mechanisms and speech articulation. In line with our hypothesis, we found reduced FA in SI in a motor network including the left anterior insula, the basal ganglia, and the upper part of the corticospinal tract. As a second main result, we found significantly reduced FA in SI in the anterior and posterior part of the corpus callosum, suggesting that intensive language training as experienced in simultaneous interpreting influences interhemispheric transfer functions. Our results might have implications for the understanding of language expertise in relation to plastic changes in the white matter architecture.

ACKNOWLEDGMENTS

The authors thank Marcus Cheetham for helpful comments on a previous version of the manuscript and Lucas Marrama for assisting in data acquisition.

Author contributions

SE conceived the study, designed the experimental paradigm, and drafted the manuscript. JH contributed to the hypothesis, to the manuscript, and performed the data analysis. MM contributed to the hypothesis, design, results discussion, and preparation of the manuscript. LJ contributed to the hypothesis, design, results, discussion, and preparation of the manuscript. All authors read and approved the final manuscript.

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3.3. Study C: Intensive Language Training and Attention Modulate the Involvement of Fronto-Parietal Regions During a non-Verbal Auditory Discrimination Task.

Full Citation:

Elmer, S., Meyer, M., Marrama, L., and Jäncke, L. Intensive language training and attention modulate the involvement of fronto-parietal regions during a non-verbal auditory discrimination task. *European Journal of Neuroscience* 34: 165-175, 2011.

3.3.1. Abstract

This event-related functional magnetic resonance imaging (fMRI) study was designed in such a manner so as to contribute to the present debate on behavioural and functional transfer effects associated with intensive language training. To address this novel issue, we measured professional simultaneous interpreters and control subjects while they performed a non-verbal auditory discrimination task that primarily relies on attention and categorization functions. The fMRI results revealed that the discrimination of the target stimuli was associated with differential blood oxygen level-dependent responses in fronto-parietal regions between the two groups, even though in-scanner behavioural results did not show significant group differences. These findings are in line with previous observations showing the contribution of fronto-parietal regions to auditory attention and categorization functions. Our results imply that language training modulates brain activity in regions involved in the top-down regulation of auditory functions.

EJN fens EUROPEAN JOURNAL OF NEUROSCIENCE

European Journal of Neuroscience, Vol. 34, pp. 165–175, 2011 doi:10.1111/j.1460-9568.2011.07728.x

COGNITIVE NEUROSCIENCE

Intensive language training and attention modulate the involvement of fronto-parietal regions during a non-verbal auditory discrimination task

Stefan Elmer,[1] Martin Meyer,[1,2] Lucas Marrama[1] and Lutz Jäncke[1]
[1]Department of Neuropsychology, Institute of Psychology, University of Zürich, Binzmühlestrasse 14/25, CH-8050 Zürich, Switzerland
[2]Center for Integrative Human Physiology, University of Zürich, Binzmühlestrasse 14/25, CH-8050 Zürich, Switzerland

Keywords: attention and categorization functions, non-verbal discrimination task, simultaneous interpreters, transfer effects

Abstract

This event-related functional magnetic resonance imaging (fMRI) study was designed in such a manner so as to contribute to the present debate on behavioural and functional transfer effects associated with intensive language training. To address this novel issue, we measured professional simultaneous interpreters and control subjects while they performed a non-verbal auditory discrimination task that primarily relies on attention and categorization functions. The fMRI results revealed that the discrimination of the target stimuli was associated with differential blood oxygen level-dependent responses in fronto-parietal regions between the two groups, even though in-scanner behavioural results did not show significant group differences. These findings are in line with previous observations showing the contribution of fronto-parietal regions to auditory attention and categorization functions. Our results imply that language training modulates brain activity in regions involved in the top-down regulation of auditory functions.

Introduction

A considerable amount of work has been performed to elucidate the brain regions that support auditory-related attention functions (Coull, 1998; Zatorre *et al.*, 1999; Hopfinger *et al.*, 2000; Jancke & Shah, 2002; Jancke *et al.*, 2003; Rinne *et al.*, 2005, 2007a,b; Degerman *et al.*, 2006; Brungart & Simpson, 2007; Baumann *et al.*, 2008; Abel, 2009), but little is known about the influence that language training has on this cognitive operation; for example, how does the language training that simultaneous interpreters (SIs) experience impact on their auditory-related attention function? The notion that intensive training in a particular domain can influence other faculties that have not been specifically trained has received considerable attention, especially in individuals who have undergone musical training. Previous researchers have demonstrated behavioural transfer effects in cognitive domains that are not necessarily directly linked to music processing in both children (Schlaug *et al.*, 2005; Magne *et al.*, 2006) and adults (Schlaug *et al.*, 2005). Such transfer effects were reported in the domain of visuospatial abilities (Brochard *et al.*, 2004), mental imagery (Aleman *et al.*, 2000), mathematical abilities (Bilhartz *et al.*, 1999), spatio-temporal reasoning (Gromko & Poorman, 1998), and verbal memory functions (Ho *et al.*, 2003).

Besides this evidence for transfer effects at the behavioural level, several electrophysiological (electroencephalographic) studies conducted with professional musicians (Nager *et al.*, 2003) and children who had received short-term (Bangert & Altenmuller, 2003) or long-term (Shahin *et al.*, 2004) musical training have indicated that musical training has an influence on the functional architecture of brain regions that are not specific only to music processing. Also, previous electroencephalographic and brain imaging studies revealed transfer effects exerted by musical training on speech processing (Tervaniemi *et al.*, 2009; Oechslin *et al.*, 2010; Elmer *et al.*, 2011). Other studies have shown that musicians are more sensitive to pitch information than are non-musicians (Schon *et al.*, 2004; Besson *et al.*, 2007; Wong *et al.*, 2007). Furthermore, there is mounting evidence showing that acoustic parameters, such as frequency, duration, and intensity, are differentially encoded during speech and music processing by musicians and laymen under conditions of different attentional demands (Tervaniemi *et al.*, 2005, 2009; Baumann *et al.*, 2008). Even though most of these studies have found evidence for both behavioural and functional transfer effects, other studies have reported functional transfer effects without behavioural evidence (Jentschke, Koelsch & Friederici, 2005; Baumann *et al.*, 2008; Oechslin *et al.*, 2010). These studies are particularly important, because they show that the functional architecture of the human brain can be altered through training that does not mandatorily entail a behavioural advantage.

Given this wealth of evidence for behavioural or functional transfer effects or both in individuals undergoing intensive musical training, the present study aimed to introduce a novel account regarding the present view regarding the present view of the relationship between language training and transfer effects. This novel account is based on the investigation of subjects who are specifically trained to convert, in 'real time', expressions in a source language into expressions with a

Correspondence: S. Elmer, as above.
E-mail: s.elmer@psychologie.uzh.ch

Received 12 January 2011, revised 22 March 2011, accepted 9 April 2011

comparable meaning in a target language, namely, SIs. Only a few previous neuroimaging (Rinne *et al.*, 2000), electrophysiological (Elmer *et al.*, 2010a; Proverbio *et al.*, 2004, 2009) and anatomical (Elmer *et al.*, 2010b) studies have shown that SIs form a suitable group for delineating the enduring effects of language training on the functional and anatomical architecture of the human brain. Furthermore, a number of behavioural studies (Daro & Fabbro, 1994; Christoffels *et al.*, 2006; Cowan, 2010) have pointed out that the engagement of executive functions, most notably auditory attention and working memory functions, is essential for performing interpretations at a professional level (Rinne *et al.*, 2000). Notably, previous work has illustrated the involvement of non-linguistic executive control mechanisms in association with language expertise, as revealed in proficient bilinguals (Abutalebi *et al.*, 2007, 2008; Abutalebi, 2008). In fact, some previous studies have linked language skills in proficient bilinguals to enhanced attention functions when comparing this group with monolingual subjects (Bialystok *et al.*, 2004; Costa *et al.*, 2008). Even though we are fully aware that bilingual subjects' language capabilities cannot be directly compared with the exceptional faculties observed in professional SIs (owing to the specific training that SIs undergo), the aforementioned behavioural results suggest a close intertwining of executive functions and language expertise. In particular, they support the notion that cognitive functions lead to benefits not only in language control mechanisms, but also in performing non-linguistic tasks (Bialystok *et al.*, 2004; Costa *et al.*, 2008). Moreover, even though outstanding evidence pointing to more efficient phonological processing in SIs is currently absent, one could speculate that individuals intensely trained to make rapid phonological distinctions with minimal errors could develop a neural architecture that supports accurate categorical distinctions of auditory stimuli. In this context, there is strong evidence suggesting that particular brain regions situated in the inferior parietal lobe (IPL) (i.e. the angular and supramarginal gyrus) are fundamentally involved in mapping a sound's structure to its phonetic representation (Ruff *et al.*, 2003; Blumstein *et al.*, 2005; Cousin *et al.*, 2007; Joanisse *et al.*, 2007; Turkeltaub & Coslett, 2010). Extending this logic further, one could expect that subjects who developed this training-related architecture in more posterior perceptual systems might rely to a lesser extent on frontal systems, in order to make top-down decisions for categorizing auditory stimuli.

We suppose that transfer effects in SIs may originate as a consequence of the cognitive requirements necessary for translating a first language into a second one, because in doing this it is necessary to attentively 'monitor' both the input language and its respective translation. In this context, we consider simultaneous interpreting to be a remarkable skill that places impressive demands on executive functions, most notably on auditory-related attention functions. Furthermore, we consider SIs as individuals who are highly trained in building phonological categorial percepts, and speculate whether this specific ability may favour the discrimination of non-verbal material as well. We designed this functional magnetic resonance imaging (fMRI) study on the basis of previous behavioural studies that pointed out the relevance of executive control functions in professional interpreting (Daro & Fabbro, 1994; Christoffels *et al.*, 2006; Cowan, 2010), in order to investigate whether long-term language training is associated with functional or behavioural transfer effects or both. To address this issue, we performed measurements on professional SIs and control subjects while they performed an auditory task requiring the attentive discrimination and categorization of target stimuli in a non-verbal environment. This sort of task requires focused attention to the target stimuli, as well as sustained attention over time (i.e. monitoring). Furthermore, in order to perform the task, subjects not only have to attentively perceive and discriminate the stimuli, but must also compare them with the respective targets. Consequently, the auditory discrimination task that we used in the present study relies on perceptual and cognitive functions, as well as on the ability to categorize auditory percepts.

Even though theories of attention differ in the conceptualization and partitioning of the single components involved (Posner & Boies, 1971; Mirsky *et al.*, 2010), a number of previous studies have converged on the notion that fronto-parietal regions are strongly involved in numerous attention tasks across different modalities (Pardo *et al.*, 1990; Zatorre *et al.*, 1999; Rinne *et al.*, 2005; Degerman *et al.*, 2006; Johnson & Zatorre, 2006). Moreover, there is evidence from imaging studies (Turkeltaub & Coslett, 2010), as well as clinical evidence (Ruff *et al.*, 2003), suggesting that regions situated in the left IPL are involved in building phonological categorical percepts. In this context, we speculate that a training-related neuronal reorganization of inferior parietal regions in SIs may be advantageous for discriminating and categorizing non-verbal auditory stimuli. In the present work, we specifically addressed the question of whether professional language training is associated with functional changes in fronto-parietal regions that have been consistently shown to be involved in attention functions and to support the categorization of auditory stimuli. Furthermore, we investigated whether these training-related architectural changes may favour the behavioural performance in the context of a non-verbal auditory discrimination task.

Materials and methods

Subjects

Twenty-six volunteers were recruited for this experiment, comprising 10 professional SIs (specifically trained and certified graduated professional SIs; six females and four males, aged 32–48 years) and 16 controls (seven females and nine males, aged 26–35 years). All of the control subjects had an academic degree. All participants had a comparable level of education (i.e. they had a university degree or were currently advanced university students). According to the Annett-Handedness Questionnaire (Annett, 1970), all subjects were consistently right-handed. Each research participant gave written consent, in accordance with this study's procedures, which were approved by the local Ethics Committee. All participants were paid for their participation. Table 1 gives an overview of the languages spoken by the subjects investigated.

Auditory stimuli

In the present experiment, we used three auditory stimuli, presented binaurally. Each stimulus consisted of two synthetic tones that overlapped in time: a sine wave (ADOBE AUDITION 1.5) and a guitar tone (FRUITY LOOP). The stimuli lasted 600 ms, and included an abrupt linear pitch modulation in the form of a frequency decrease, which took place after 300 ms (Fig. 1). The first stimulus [sinus change (SC)] was composed of both a constant guitar tone (C5 American notation) and a sine wave that changed in frequency after 300 ms from 625 Hz to 600 Hz. The second stimulus [guitar change (GC)] was composed of a constant sine wave tone (625 Hz) and an overlapping guitar tone that changed its frequency after 300 ms from C5 to C4 (American notation). The third stimulus was composed of a guitar tone (C5–C4, American notation) and a sine wave (625–600 Hz) tone, both of which changed in frequency after 300 ms [both change (BC)]. All sound files were digitized at a 16-bit/44.1-kHz sampling rate, and were normalized in amplitude (ADOBE AUDITION 1.5).

TABLE 1. The different languages spoken by the subjects

Subjects	Languages spoken
SI 1	German, French, English
SI 2	German, Spanish, French, English, Portuguese
SI 3	German, French, English, Polish
SI 4	German, Italian, French, English
SI 5	German, French, Italian, English, Spanish, Portuguese
SI 6	German, English, French, Spanish, Italian
SI 7	German, English, Italian, French, Romanian
SI 8	German, English, Spanish, French
SI 9	German, English, French
SI 10	German, English, French, Spanish, Italian
C 1	German, French, English, Italian
C 2	German, French, English
C 3	German, Italian, French, English
C 4	German, Spanish, English
C 5	German, French, Italian, English
C 6	German, French, Italian, English
C 7	German, Dutch, Portuguese, English
C 8	German, French, English, Spanish
C 9	German, English, French
C 10	German, English, French
C 11	German, Italian, French, English
C 12	German, French, English, Israeli
C 13	German, French, Italian, English
C 14	German, French, Spanish, English, Potuguese
C 15	German, French, English
C 16	German, French, Italian, Spanish, English

C, control; SI, simultaneous interpreters.

Pre-scanning training

Before application of the fMRI protocol, the auditory stimuli were presented to every subject outside the scanner via headphones until a clear discrimination was achieved. Moreover, each subject underwent a short computer-based training session to confirm their ability to discriminate the three auditory stimuli (total of 18 stimuli: six SC, six GC, and six BC) before entering the scanner. If adequate performance was not observed (every subject had to discriminate at least four of the six stimuli from each category), then training was repeated. After this short training, participants were permitted to participate in the main fMRI session.

Experimental procedure

Series of stimuli were assigned to three successive runs; each run comprised all three stimuli (SC, GC, and BC), but corresponded to different discrimination conditions (SC, GC, and BC). In each of the three runs, one particular stimulus had to be actively discriminated (discrimination) and the other two stimuli acted as non-target stimuli (monitoring). In other words, during each run, the participants had to focus their attention only on a particular stimulus and to discern the particular stimulus at hand by pressing a response button every time that it was heard. This task required selective attention to the target stimuli (discrimination), as well as sustained attention over time (monitoring). The term 'monitoring' means that no overt judgement was required; however, it does not imply that listening to these lists is a passive cognitive process. Furthermore, in order to perform this non-verbal discrimination task, subjects must not only focus their attention on the stimuli, but must also compare them with the respective targets. Consequently, this auditory discrimination task relies on perceptual and cognitive functions (mainly attention functions), as well as on the ability to categorize auditory percepts.

The three runs were counterbalanced across subjects and groups. Each of the three runs included a series of 60 stimuli (20 SC, 20 GC, and 20 BC) and 177 empty trials (without acoustic stimulation), which were used to define baseline and to avoid expectancy. The auditory stimuli were jittered with an interstimulus interval corresponding to two to five repetition times (TRs). We used an acquisition time of 2 s and a TR of 3 s, in order to avoid an overlap between scanner noise and stimulus presentation (Jancke *et al.*, 2002). Consequently, the auditory stimuli could be presented in silence during a 1-s gap (300 ms of silence, 600 ms of stimulus presentation, and 300 ms of silence). Both the auditory stimulus presentation and the collection of behavioural responses were controlled by PRESENTATION software (Version 0.70; Neurobehavioral Systems, USA).

fMRI data acquisition and processing

During scanning, the participants were instructed to keep their eyes open and to focus on the fixation cross presented on the screen. Binaural auditory stimuli were presented by a digital playback system

TABLE 2. The maxima of all significant clusters revealed by the SPM5 full factorial design (k = 30 voxels, $P < 0.001$, uncorrected), according to the computed two-way ANOVAs; the main effects (MEs: discrimination, monitoring, and group) have been given anatomical labels

				Coordinates LH			Coordinates RH		
Condition	Regions	Voxels	F	x	y	z	x	y	z
ME group									
Discrimination	AG	50	17.02	−54	−70	24			
	FO	49	16.93				52	12	24
	IPL	62	16.33	−34	−54	−38			
Monitoring	FO	88	18.23				52	14	28
	PC	31	17.76				10	−66	34
	AG	40	14.94	−52	−70	24			
	IPL	43	14.93	−32	−58	38			
ME discrimination/ monitoring									
Discrimination	PU	76	15.78	−30	−18	4			
	HG	44					46	−34	12
Monitoring	RO	98	12.71	−46	−26	20			
	PCING	69	11.71				14	−46	18
	PG	51	10.19	−40	−26	46			

LH, left hemisphere; RH, right hemisphere; RO, rolandic operculum; PCING, posterior cingulum.

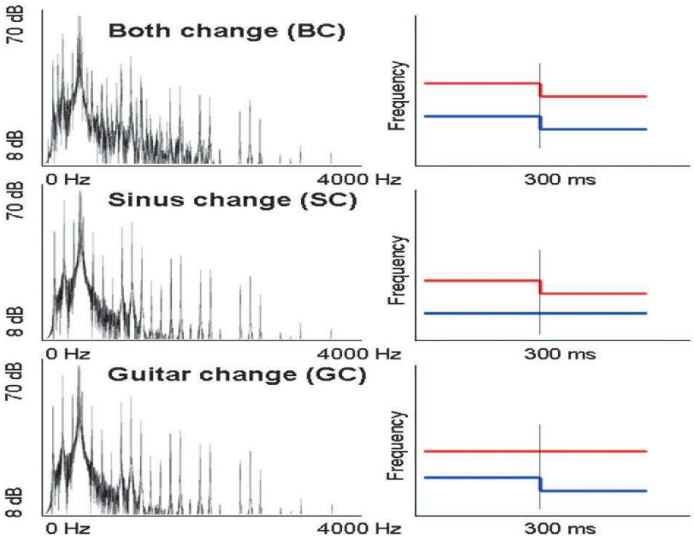

FIG. 1. The left part of the figure shows the spectra of the auditory stimuli. The schemata on the right side show the time course of the two tones (red, sine wave tone; blue, guitar tone). Respective pitch modulations are displayed.

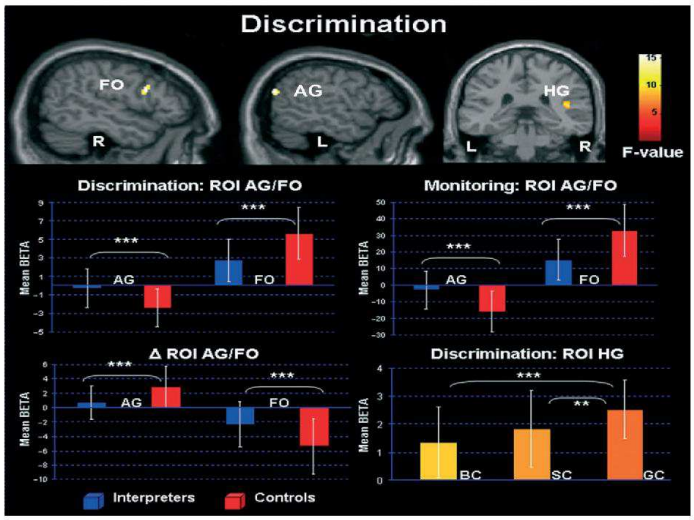

FIG. 2. The significant results of a full factorial design performed with SPM5. The upper parasagittal illustrations (left and middle images) show the main effect of group. The coronal image on the right shows the main effect of the discrimination condition. R, right; L, left. The four plots in the lower part of the figure show the mean β-values extracted from the AG, FO and HG ROIs. Δ indicates the difference in mean β-values (target stimuli minus non-target stimuli) related to the AG and FO ROIs. $^{***}P < 0.001$; $^{**}P < 0.01$. The error bars show standard errors.

including a high-frequency shielded transducer system. The acoustic transmission system included a piezoelectric loudspeaker, which enabled the transmission of strong sound pressure levels (105 dB) with excellent attenuation characteristics (Jancke *et al.*, 2001). Furthermore, earplugs were used to attenuate detrimental scanner noise.

A Philips Intera 3-T whole-body MR unit (Philips Medical Systems, Best, the Netherlands), at the University Hospital Zurich, which is equipped with an eight-channel Philips SENSE head coil, was used to acquire functional magnetic resonance images. Functional data were obtained from 240 whole-head scans per run (each run lasted about

12 min) with a Sensitivity Encoded (SENSE) single-shot echoplanar imaging technique (TR, 3000 ms; acquisition time, 2000 ms; echo time, 35 ms; flip angle, 78°; field of view, 220 mm; acquisition matrix, 80 × 80; 33 transverse slices; voxel size, 1.72 × 1.72 × 4.00 mm).

fMRI data analysis was performed with MATLAB 2006b (Mathworks, Natick, MA, USA) and the SPM5 software package (Institute of Neurology, London, UK). All images were realigned to the first image of the first run, spatially normalized into standard stereotactic MNI space (EPI template provided by the Montreal Neurological Institute), interpolated to a voxel size of 2.00 × 2.00 × 2.00 mm, and spatially smoothed using an 8-mm full-width-at-half-maximum Gaussian kernel.

Statistical analyses

Statistical analysis was based on the general linear model. Because of the experimental design, an event-related analysis was conducted. The standardized canonical haemodynamic response function and its temporal derivate were applied to model the blood oxygen level-dependent (BOLD) response to each of the three auditory stimuli. The model that we used included separate regressors for each of the auditory conditions, which were applied separately for each run. The first level of analysis involved implementing the comparisons of interest as linear contrasts against baseline (empty trials). The resulting set of voxel values for each contrast constitutes a statistical parametric map of the *T*-statistic.

For the group-level analysis, we specified the SPM5 factorial design using two independent variables; this resulted in two independent 2 × 3 ANOVAs, one related to the discrimination condition (two group levels – SIs and controls; three discrimination levels – SC, GC, and BC), and one related to the monitoring condition (two group levels – SIs and controls; three monitoring levels – SC, GC and BC). Only significant clusters of activation from the ANOVA results (SPM5) were considered (uncorrected α-level = 0.001; $k \geq 30$). To disentangle discrimination from monitoring, we also performed *post hoc* region of interest (ROI) analyses, using spheres centred at maximal local *F*-values (resulting from the ANOVAs). The software MARSBAR (http://sourceforge.net/projects/marsbar/files/marsbar/) was used to define 7-mm radius spherical ROIs [ROI frontal operculum (FO) (52 12 24); ROI angular gyrus (AG) (–54 –70 24); and ROI Heschl's gyrus (HG) (46 –34 12)]. Mean β-values were read out by in-house-programmed MATLAB scripts (http://www.mathworks.com/), and were further analysed by the use of *t*-tests (SPSS; http://www.spss.com/). All *post hoc* tests performed with the data extracted from the ROIs were corrected for multiple comparisons with the Bonferroni procedure. As the two groups significantly differed in age, we also computed simple regressions, in order to disentangle the influence of age from the activation patterns related to the three discrimination conditions.

Results

Behavioural data

The behavioural responses of four volunteers (two SIs and two controls) could not be recorded, owing to technical problems. The descriptive analyses of the collected behavioural responses suggest that the two groups were able to perform above chance levels on the three discrimination conditions (mean of correct detected stimuli: SIs, BC 71.8%, SC 88.1%, and GC 95%; controls, BC 73.2%, SC 80.7%, and GC 82.8%). To statistically evaluate the behavioural data collected during scanning, we performed a 2 × 3 factorial analysis (ANOVA, repeated measures) across the two groups. The numbers of correct responses during the three discrimination conditions served as the within-subject factors.

The outcome of this statistical analysis yielded a main discrimination condition effect (discrimination, $F_{1,\ 20} = 5.201$, $P = 0.034$). *Post hoc* *t*-tests (Bonferroni-corrected threshold for $\alpha = 0.05$, $P = 0.016$) were computed to further explore the main discrimination condition effect, which we revealed in the previous ANOVA analysis. This procedure revealed a significant difference between the discrimination of BC and SC stimuli (BC vs. SC, $t_{21} = -2.518$, $P = 0.01$). In addition, the comparison between BC and GC showed a statistical trend slightly above the Bonferroni-corrected threshold ($t_{21} = -2.110$, $P = 0.023$). In summary, the behavioural results (hit percentage) collected inside the scanner showed that volunteers experienced more difficulty during the BC condition than during the SC and GC discrimination conditions. We then evaluated the latency of response speed within the scanner by performing a 2 × 3 factorial analysis (ANOVA, repeated measures) across the two groups. The reaction times of the subjects during the three discrimination conditions served as within-subject factors. This analysis did not yield significant main or interaction effects.

Brain responses associated with the discrimination conditions

In order to determine the brain regions supporting the active discrimination of the target stimuli, we performed a 2 × 3 ANOVA (SPM5, full factorial design) that included the target stimuli and both groups as independent variables. The outcome of the ANOVA computation yielded a main effect of group and a main effect of discrimination. All significant clusters of activation maxima representing the main effects are shown in Table 2. The main effect of group was characterized by activations in the right FO, the left AG, and the left IPL. The same statistical analysis also revealed a main effect of discrimination condition in the left putamen (PU) and in the right HG.

Brain responses associated with monitoring

In order to determine the brain responses related to monitoring that are independent of the discrimination of the stimuli, we performed a 2 × 3 ANOVA (SPM5, full factorial design) that included the non-target stimuli and both groups as independent variables. All significant clusters of maxima of activation representing the main effects are listed in Table 2. The main effect of group was characterized by differential responses between the two groups of the right FO and the precuneus (PC). Furthermore, the main effect of group reflected differential activation patterns between the two groups in the left AG and the IPL. The results of this statistical procedure also revealed a main effect of monitoring in the left-sided RO, postcentral gyrus (PG), and right posterior cingulum.

ROI analyses: disentangling discrimination-related responses from monitoring-related responses

The outcome of the two ANOVAs (SPM5) that were computed with the target (discrimination) and non-target (monitoring) stimuli showed group differences in identical anatomical regions, namely, the AG, FO, and IPL. In order to disentangle the responses associated with the active discrimination of the target stimuli (discrimination) from those induced by the non-target stimuli (monitoring), we performed *post hoc* ROI analyses. The ROIs were centred at the maximal *F*-values of

cluster activation (resulting from the ANOVA analyses). We extracted mean β-values from ROI AG (–54 –70 24) and ROI FO (52 12 24) by adopting spherical ROIs with a radius of 7 mm. In order to disentangle the confounding influence of monitoring, we subtracted mean β-values related to monitoring from those related to the active discrimination of the stimuli.

Figure 2 shows that the main group effect arising from the two ANOVAs can be attributed to larger mean β-values (extracted from ROIs AG and FO) in the control group. In particular, the controls showed more negative mean β-values in the left AG and more positive values in the right FO during both the discrimination and the monitoring conditions. Figure 3 shows that the negative β-values extracted from ROI AG are congruent with a negative devolution of the percentage fMRI signal change, thereby, reflecting a signal depression in comparison with the baseline. Furthermore, Fig. 2 shows that the monitoring condition elicited significantly stronger brain responses than the discrimination condition. The outcome of the subtraction procedure (mean β-values related to active discrimination minus mean β-values related to monitoring) clearly shows that the fMRI signal change in the left AG and in the right FO was modulated by the task (applied as a function of language expertise). Table 3 shows the statistical results of the *post hoc* ROI analyses.

ROI analyses: disentangling the main effect of discrimination

We also performed *post hoc* ROI analyses because we wished to further explore the main effect produced by the discrimination condition (irrespective of group). This analysis revealed a main effect of discrimination in the right HG while the subjects performed the three tasks. What contribution do the three discrimination conditions make to the activation of the right HG? In order to answer this important question, we performed ROI analyses by adopting a sphere with a radius of 7 mm centred at the maximal *F*-value of cluster activation (resulting from the ANOVA analysis). Undoubtedly, the main effect of discrimination is not confounded by the monitoring condition, as the ANOVA previously computed on the non-target stimuli (monitoring) did not reveal a comparable main effect. Figure 2 shows mean β-values extracted from ROI HG for each discrimination condition, collapsed over the two groups. Accordingly, the GC discrimination task yielded stronger activations in the right-sided HG than the SC and BC tasks did. Table 3 shows the statistical results of the *post hoc* ROI analyses.

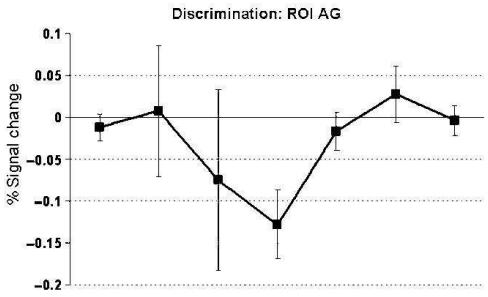

FIG. 3. The percentage of signal change in the AG, in relation to the baseline while SIs performed the discrimination task. Each data point corresponds to one of seven consecutive volume acquisitions. The error bars illustrate standard errors.

Regression with age

As the two groups differed in age, we computed simple regressions of the fMRI-related signal corresponding to the three discrimination conditions with age. This analysis yielded a positive correlation between the fMRI signal associated with the BC condition and age at the medial border of the left supramarginal gyrus that was proximate to the optic radiation (–32 –54 14). We also revealed a negative correlation between the fMRI signal associated with the SC condition and age in the left superior frontal gyrus (–14 14 56). For all regressions, we used an uncorrected α-level of 0.001 and a cluster extent of $k \geq 30$).

Discussion

General discussion

Previous theoretical work (Daro & Fabbro, 1994; Moser-Mercer, 1997; Christoffels *et al.*, 2006; Cowan, 2010) has suggested that the performance of a professional SI is strongly related to the integrity of the control of executive functions. In particular, the abilities to monitor, shift and distribute attention to different parallel tasks have been identified as fundamental processing requirements for simultaneous interpreting. In fact, this exceptional performance strongly relies on the cognitive requirements necessary for translating a first language into a second one while concomitantly monitoring both the input language and its respective translation. Furthermore, we speculated that individuals intensely trained to make rapid phonological distinctions with minimal errors may have developed a neural architecture that supports accurate categorical distinctions of auditory stimuli. As there is imaging evidence (Turkeltaub & Coslett, 2010) as well as clinical evidence (Ruff *et al.*, 2003) suggesting that regions situated in

TABLE 3. The statistical results (*t*-tests, one-tailed) of the *post hoc* ROI analyses in the ROIs AG, FO, and HG for each condition

Condition	ROI	Contrast	*t*-value	d.f.	*P*-value
Discrimination	AG	SI vs. C	4.471	76	0.0001
	FO	SI vs. C	−4.727	76	0.0001
	HG	BC vs. SC	−1.833	25	0.039
		BC vs. GC	−4.828	25	0.0001
		FS vs. GC	−3.260	25	0.0015
Monitoring	AG	SI vs. C	4.602	76	0.0001
	FO	SI vs. C	−5.087	76	0.0001
Discrimination minus monitoring	AG	SI vs. C	−3.444	76	0.0001
	FO	SI vs. C	3.636	76	0.0001

C, control; d.f., degrees of freedom; SI, simultaneous interpreters.

the left IPL are involved in building phonological categorical percepts, we speculated that a training-related neuronal reorganization of these regions may also be advantageous for categorizing non-verbal auditory stimuli.

In keeping with this, we hypothesized that these extensively trained attention and categorization functions should be manifested functionally, behaviourally or both functionally and behaviourally in SIs; that is, not only in the domain of language processing, but also in other non-linguistic domains. Our current findings favour the notion that the discrimination of non-linguistic sound attributes leads to differential involvement of fronto-parietal networks between the two groups. Even though the different brain responses between the two groups were not accompanied by differences in the behavioural data, our results are in line with those of previous studies, which have shown that the fronto-parietal areas play a specific role in the modulation of attention functions across different modalities (Pardo *et al.*, 1991; Zatorre *et al.*, 1999; Rinne *et al.*, 2005; Degerman *et al.*, 2006; Johnson & Zatorre, 2006). Otherwise, these results could also be interpreted as indicating that SIs developed a neural architecture in the left IPL (AG) that supports accurate categorical distinctions of auditory stimuli. Consequently, it is plausible that persons who, through training, developed this architecture in more posterior perceptual systems might rely to a lesser extent on frontal control systems when making top-down decisions about the nature of auditory stimuli.

Behavioural data

The statistical evaluation of the behavioural data collected inside the scanner revealed that the subjects recognized the target stimuli at a rate that is above chance, and that the two groups did not differ significantly in either the number of correct responses or in reaction time. In addition, the statistical results showed that the two groups experienced more difficulty with the BC discrimination condition. The statistical analyses performed on the behavioural data favour the view that the lower number of correctly detected target stimuli during the BC condition was related to the difficulty of this specific task. This is supported by the fact that, during this specific condition, both signals (i.e. the sine wave and the guitar tone) simultaneously decreased in frequency after 300 ms. Therefore, the acoustic signal changes were less salient and more difficult to detect. Further evidence for the notion that the BC condition was more demanding is provided by the fact that, during the SC and GC conditions, one of the two signals remained constant over time. This implies that the constant signal acted as a background and that the changing signal popped out in the foreground. During the BC condition, this foreground–background differentiation was not possible; thus, discrimination was more demanding.

Functional but not behavioural group differences

An important point that must be addressed concerns the meaning of the functional transfer effects that occur in the face of no behavioural difference between the two groups. Whereas several studies consistently found a link between functional and behavioural measurements (Schon *et al.*, 2004; Besson *et al.*, 2007), other work only reported functional transfer effects (Jentschke *et al.*, 2005; Oechslin *et al.*, 2010). In the present study, we did not find behavioural differences between the two groups; nonetheless, this does not actually contrast with the notion that language training can modulate the functional architecture of brain regions that support top-down functions in the context of auditory processing. For example, this possibility is strongly supported by previous studies that were dedicated to the investigation of auditory-related cognitive functions in older and younger subjects. In fact, some of these studies showed differential responses in frontal areas even though the two groups did not differ in terms of behavioural performance (Wong *et al.*, 2009). These results favour the view that the functional differences between older and younger subjects reflect compensatory activity that is responsible for maintaining the level of performance of older subjects at an equivalent level to that of the younger subjects.

Angular gyrus (AG)

The present study was specifically designed to investigate whether long-term language training, as experienced by SIs, favours functional or behavioural transfer effects, or both, beyond the domain specifically trained. Transfer effects were demonstrated in previous studies of professional musicians who underwent intensive musical training. In particular, we expected to find that the long-term training necessary to become a SI would strengthen auditory-related cognitive functions by tuning sensory mechanisms to relevant acoustic features. The between-group comparison of the functional maps associated with the discrimination of the target stimuli revealed increased BOLD signals in the left AG in the SI group, irrespective of the brain responses induced by the acoustic perception per se. These enhanced brain responses in the SI group are indicative of alterations in the functional architecture involved in the top-down regulation of auditory processing (mainly attention and auditory categorization functions) in conjunction with professional language training.

Meanwhile, there is an impressive number of brain imaging studies providing compelling evidence for the functional contribution made by the IPL in detecting events in the sensory environment that are under the influence of attentional functions (Kiehl *et al.*, 2005). In fact, this brain region has been shown to support voluntary attention and target detection mechanisms in the auditory (Brungart & Simpson, 2007; Knight *et al.*, 1989; Linden *et al.*, 1999; Shomstein & Yantis, 2006) and visual (Marois *et al.*, 2000; Rushworth *et al.*, 2001) modalities. Further evidence supporting the functional contribution of the IPL to attention functions comes from clinical studies performed with patients affected by focal cortical lesions (Coull, 1998; Friedrich *et al.*, 1998; Ro *et al.*, 1998; Vallar, 1998).

Top-down modulations of audition in the form of attention functions were previously estimated by adopting auditory discrimination tasks under both binaural and dichotic listening conditions (Pugh *et al.*, 1996; Hall *et al.*, 2000; Linden *et al.*, 1999; Rinne *et al.*, 2007a,b) and by using either verbal (Pugh *et al.*, 1996; Vouloumanos *et al.*, 2001) or non-verbal (Rinne *et al.*, 2007a,b; Linden *et al.*, 1999) material. In this context, inferior parietal areas were not only associated with auditory target detection (Vouloumanos *et al.*, 2001; Hall *et al.*, 2000) and voluntary control of attention (Pugh *et al.*, 1996), but were also shown to be engaged in the processing of sound changes, as well as the processing of novel sounds in the auditory environment (Molholm *et al.*, 2005). The aforementioned results, together with our finding of differential responses in the left IPL (AG) between the two groups during an auditory discrimination task, may indicate that language training is accompanied by plastic alterations in regions subserving attention functions. This makes sense in that attention functions represent a fundamental cognitive requirement for performing simultaneous translations.

At this point, it is important to address an alternative explanation concerning the differential left-sided AG involvement between the two groups. Notably, in addition to relying on attentional abilities, the auditory discrimination task that we used also relies on categorization

mechanisms. In fact, in order to accomplish the task, the subjects not only had to monitor the stimuli and to focus on the targets, but also had to properly perceive the acoustic material and categorize it into its respective auditory percepts. Functional neuroimaging [consider the meta-analysis from Turkeltaub & Coslett (2010)] and clinical (Ruff *et al.*, 2003) studies provide evidence that the AG is fundamentally involved in building phonological categorical percepts. In particular, previous work suggests that the left IPL in general, and the AG in particular, are engaged in subserving the categorization and discrimination of phonetic information in speech (Joanisse *et al.*, 2007). For example, Blumstein *et al.* (2005) explored the neural systems that underlie the perception of phonetic category structure by investigating the perception of a voice-onset-time continuum in a phonetic categorization task. The notion that the left AG was particularly responsive to the 'best fit' to a phonetic category (significantly greater activation for endpoint stimuli than for within-category stimuli) favours the view that this brain region is involved in mapping sound structure to its phonetic representation. By using a visually presented rhyme detection task, Cousin *et al.* (2007) obtained similar results that further support the contribution made by the left AG to phonetic categorization.

Certainly, it ispossible that the ability to make rapid phonological distinctions, with minimal errors, could be associated with cortical reorganization in brain regions such as the AG, an area that is specifically devoted to this purpose [consider the meta-analysis from Turkeltaub & Coslett (2010)]. Extending this logic further, a person who, through training, developed this architecture in more posterior perceptual systems might rely to a lesser extent on frontal control systems when making top-down decisions about the nature of auditory stimuli. This framework may account for the results produced by our study without specifically invoking attention as the particular domain of cognition affected.

The fact that we found stronger BOLD responses of the AG in the SI group during processing of target as well as of non-target stimuli is not surprising, as both conditions (i.e. discrimination and monitoring) rely on attentional and categorial functions. These results may indicate that the training involved in becoming an interpreter is associated with functional adaptations in brain regions that support a more general structure–function principle. This functional transformation could be the consequence of dynamic requirements (i.e. attention and categorization functions) that are necessary for performing professional interpretations.

Frontal operculum (FO)

It is undisputed that the architecture of the cerebral cortex is organized in a hierarchical manner. The base of this cortical organization is composed of regions that support sensory and motor functions. In contrast, regions with later phylogenetic and ontogenetic development, such as the prefrontal cortex, regulate information processing and response selection in situations where routine mechanisms are unavailable for task performance. In other words, the prefrontal cortex is crucial in subserving higher cognitive functions, including attention, working memory, and inhibition (Fuster, 2001). Interestingly, all of these cognitive functions are strongly involved in simultaneous interpreting. In addition, previous neuroimaging studies have demonstrated that prefrontal cortical regions are strongly involved in the top-down regulation of auditory processing (Jancke *et al.*, 2002; Binder *et al.*, 2004; Halpern *et al.*, 2004; Lewis *et al.*, 2004), because they direct the sensory system via attention (Roland, 1982) and memory processes (Naatanen, 1991; Schroger, 1996).

In line with our results, similar training-related neuronal changes in regions that are strongly involved in controlling executive functions as a function of expertise are supported by previous studies that investigated individuals undergoing intensive musical training (Bialystok & Depape, 2009) and bilingual individuals (Festman *et al.*, 2010). As regards bilingual individuals, recent research based on comparisons between bilingual and monolingual subjects (Bialystok *et al.*, 2004; Costa *et al.*, 2008) indicates that language skills are accompanied by altered cognitive control functions involved in controlling interferences between the different languages being spoken. Furthermore, a recent behavioural investigation (Festman *et al.*, 2010) revealed that bilinguals with strong language control abilities (i.e. non-switchers) show advantages in controlling executive functions as compared with bilinguals who have weaker control abilities (i.e. switchers). Even though we are fully aware that SIs cannot be directly compared with bilingual subjects, because of the intensive training that SIs have experienced, there are some noteworthy parallels between the two groups. In fact, both bilingual subjects and SIs rely on the integrity of executive functions, namely, attention, inhibition, working memory, and language switching mechanisms (Rinne *et al.*, 2000; Proverbio *et al.*, 2004, 2009; Abutalebi *et al.*, 2007, 2008; Abutalebi, 2008; Elmer *et al.*, 2010b).

Our results provide evidence for the notion that SIs rely to a lesser extent on frontal control systems when making top-down decisions about the nature of auditory stimuli. In particular, we propose that an anterior-to-posterior shift of cognitive functions can be advantageous, as it relieves frontal functions, which are strongly implicated in interpreting (Rinne *et al.*, 2000), from an additional cognitive load. Longitudinal studies conducted with interpreting students may be helpful, in order to gain further insights into the specific aspects of this anterior-to-posterior functional reorganization process.

Heschl's gyrus (HG)

As an interesting secondary result, the full factorial design adopted in this study revealed a main discrimination effect in the right HG that is independent of group. A *post hoc* ROI analysis in this specific region showed that the main discrimination effect was associated with stronger brain responses during the detection of the GC targets. This result is comparable with those of former studies, which have shown that the right primary auditory cortex is specifically endowed with the ability to discriminate pitch attributes (Johnsrude *et al.*, 2000; Petkov *et al.*, 2004; Tramo *et al.*, 2005), and that frequency-selective neurons in the primary auditory cortex and surrounding cortical fields play a critical role in the discrimination of fine-graded pitch modulations (Tramo *et al.*, 2005). This result is relevant, because it demonstrates that the primary auditory cortex can be selectively recruited by top-down mechanisms during an auditory discrimination task, irrespective of language expertise.

As the functional involvement of the right HG was altered as a function of the stimulus attributes to be discriminated, it is plausible that the two groups (both consisting of musically untrained subjects) adopted a similar strategy to detect the GC stimuli. It has been previously shown by Schneider *et al.*, (2005) that the pitch of instrumental sounds can be perceived by decoding either the fundamental pitch (keynote) or the spectral aspects of the stimuli. In particular, Schneider *et al.*, (2005) demonstrated that fundamental pitch listening relies on left-sided auditory cortex functions; in contrast, spectral pitch listening relies on right-sided auditory cortex functions. Consequently, we interpret the stronger responses that we found in the right HG (independently of group) as a processing

strategy (spectral listening) employed by non-musicians when performing the GC discrimination task.

Even if the subject adopted a similar strategy in order to detect the GC stimuli, a comparable effect could also be expected during the BC condition, because the guitar tone also changes in pitch. Otherwise, when we consider the behavioural data collected inside the scanner, it becomes evident that all of the subjects experienced more difficulty in detecting the BC stimuli than the GC stimuli. This significant behavioural effect may, in part, explain the stronger recruitment of the HG during the GC discrimination condition. In fact, considering the nature of the task adopted, this result suggests that the right HG is indeed functionally involved in the discrimination of instrumental pitch changes, but only when these changes are salient and can be clearly discriminated.

Age difference and brain responses

As the two groups investigated in the present study differed in age, one could argue that the age variable may have influenced the data; however, by employing regression analyses, we showed that brain responses in the left AG and in the right FO did not correlate with age. Furthermore, there is evidence showing that aging is often associated with enhanced, and not reduced, responsiveness in prefrontal brain regions. For example, Fernandes *et al.* (2006) used the fMRI technique in order to measure brain activity in younger (mean age, 26 years) and older (mean age, 71 years) adults while they were engaged in an auditory recognition task that strongly relied on executive functions. In this context, not only did the older subjects show more activity in the dorsolateral prefrontal cortex, but this activity was positively correlated with their behavioural performance. In a further study, Wong *et al.* (2009) investigated the processing of spoken language in noisy environments in a sample of younger (mean age, 21 years) and older (mean age, 67 years) subjects. In line with the results of Fernandes *et al.*, the authors found enhanced activity in prefrontal areas in older subjects, even though the behavioural performance did not differ between the two groups.

As regards tasks that more specifically rely on auditory attention and categorization mechanisms, there is electrophysiological evidence showing that frontal lobe functions may alter during normal aging (Friedman *et al.*, 1997; Fabiani *et al.*, 1998). In particular, the fact that older subjects tend to show an enhanced frontal P300 effect in comparison with younger subjects favours the view that older adults continue to use prefrontal processes for transforming stimuli that should have already been encoded and categorized (Friedman *et al.*, 1997). Taken together, these previous observations consistently show enhanced prefrontal activity in older subjects during auditory-related attention, perception and categorization tasks, probably reflecting compensatory mechanisms. In the present study, we found exactly the reverse pattern; namely, older subjects (SIs) were associated with less prefrontal activity. This observation and the regression analyses that we performed strongly argue against the notion that age differences between the two groups may have influenced the data in some direction.

Conclusions

Previous investigations have shown that the exceptional language proficiency observed in professional SIs is accompanied by functional adaptations of brain regions that are known to be involved in different aspects of language processing (Rinne *et al.*, 2000; Proverbio *et al.*, 2004, 2009; Elmer *et al.*, 2010a,b). In the present work, we addressed two novel research questions, namely, whether long-term language training influences the functional architecture that supports the discrimination of non-verbal stimulus attributes, and whether such functional reorganization favours the behavioural performance. In line with our hypothesis, we found evidence for a modulation of fronto-parietal brain regions as a function of language expertise, even though the behavioural data did not differ between the two groups. Our results imply that language training modulates brain activity in regions involved in the top-down regulation of auditory functions.

Acknowledgements

The Schweizer National Fonds (Swiss National Foundation), SNF grant 320030–120666, supported Stefan Elmer, Martin Meyer and Lutz Jäncke during the preparation of this manuscript. We thank Lucas Marrama for assistance in collecting the fMRI data, and Sarah McCourt-Meyer for comments on the previous version of the manuscript.

Abbreviations

AG, angular gyrus; BC, both change; BOLD, blood oxygen level-dependent; fMRI, functional magnetic resonance imaging; FO, frontal operculum; GC, guitar change; HG, Heschl's gyrus; IPL, inferior parietal lobe; PC, precuneus; PCING, posterior cingulate; PG, postcentral gyrus; PU, putamen; ROI, region of interest; SC, sinus change; SI, simultaneous interpreter; TR, repetition time.

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4. DISCUSSION OF THE SINGLE STUDIES

The goal of the present Ph.D. thesis was to evaluate the SIs's brain as a model for neuroplasticity as well as to investigate putative transfer effects originating from language training. With this purpose in mind, I performed three studies by using different methodologies and by focussing on different research questions. The results of these three studies have already been extensively discussed in the original published works. Hence, in turn I will only shortly summarize and discuss the main results.

4.1. Study A

Study A entitled *"Simultaneous Interpreters as a Model for Neuronal Adaptation in the Domain of Language Processing"* was designed to investigate whether professional language training as experienced by SIs has an influence on brain responses during a lexical-decision task within and across languages. Furthermore, a second goal of this EEG study was to introduce the SIs' brain as a suitable model for examining neuroplasticity in multilingual subjects, while at the same time controlling for the influence of proficiency and age of acquisition, both indeed variables which have previously been shown to have a strong influence on the cortical organization of language processing (Perani et al., 1998). During EEG measurements the subjects were instructed to judge whether word pairs presented in the German (L1) and English (L2) language (mixed and unmixed conditions) were either semantically related or not. This EEG study revealed two main findings. First, the electrophysiological data provide evidence for a faster access to lexical-semantic knowledge in the SIs group while processing semantically-unrelated words within L1

and L2, as well as during the incongruent German-English condition. This faster lexical access in the SIs group was characterized by increased brain responses which were restricted to latency bands overlapping with the onset of the N400 component. Second, during the congruent German-English condition the SIs showed tonic increased brain responses which extended over the entire period of lexical-semantic processing and were not restricted to the onset of the N400 component. Since in this specific case the tonic increased brain responses are most unlikely to reflect faster lexical access, results were interpreted as indicating that professional SIs engage more cognitive resources for processing semantically related word pairs when presented in the opposite direction as usually trained. Since the two groups we measured were matched in terms of age, age of second language acquisition, amount of exposure to L2, and L2 proficiency, results were interpreted as indicating an altered training-related sensitivity to lexical-semantic processing within and across L1 and L2.

Surprisingly, we did not find differential N400 responses between the two groups while processing word pairs in the language direction specifically trained by the SIs (i.e., during the English-German condition). This may imply that the expertise of SIs is principally manifest during sentence and not mandatorily during single-words processing, the former being indeed a more complex task which engages more cognitive resources. Consequently, we cannot exclude that the group differences we revealed in the present study rather reflect unspecific training effects than expertise per se and, that the expertise of SIs is more likely associated with an optimized engagement of cognitive functions like attention, inhibition, or working memory functions. This line of argumentation is supported by two seminal works of Abutalebi

and co-workers (Abutalebi et al., 2007; Abutalebi et al., 2009) who postulated that language expertise has a stronger impact on the engagement of extra-linguistic brain functions which are necessary for controlling the different languages in use, rather than on language representation per se. Furthermore, an alternative explanation for the lack of electrophysiological differences between the two groups during the intensively trained English-German condition may be that it would be to demanding for SIs to translate every single word they hear. In fact, it was previously proposed that SIs semantically integrate the acoustic stream in large-scale time windows rather than translating each single word (Proverbio et al., 2004).

Finally, I can only speculate about the reason for the somewhat inconsistent results we observed while the subjects performed the task in the opposite direction as usually trained by the SIs, namely during the German-English condition. As described above, we provided evidence for a faster lexical access in the SIs group, which was reflected by an increased negativity and restricted to the onset of the N400 response, while processing incongruent German-English words. Otherwise, while processing congruent trials of the same condition, the experts showed tonic increased N400 responses in a broad time window ranging from 300 to 500 ms, and therefore rather indicating the engagement of additional cognitive resources necessary for performing the task than efficiency. In this context, it is plausible to think that individuals who are specifically trained to consistently translate meaningful sentences from English to German will encounter more difficulties when the source and target languages are inverted, but only when the words are presented in a meaningful and therefore habitual context. This may be advantageous for avoiding interferences and language switching while interpreting from the English to the

German language. Certainly, further studies performed with larger samples of subjects on the word- as well as on the sentence-level are necessary to confirm these hypotheses.

4.2. Study B

In **Study B** entitled *"Differential Language Expertise Related to White Matter Architecture in Regions Subserving Sensory-Motor Coupling, Articulation, and Interhemispheric Transfer"* we investigated white matter plasticity as a function of language training and expertise. In this context, we reasoned that simultaneous interpreting places high demands on cognitive and motor control mechanisms, which are necessary for converting quasi in "real time" a source language into a target language with minimal errors. In particular, basing on previous neuroimaging (Wise et al., 1999) and lesion studies (Bates et al., 2003; Dronkers, 1996) conducted with patients suffering from articulation disorders as well as on data collected from healthy subjects during over speech production (Eickhoff et al., 2009), we expected to find evidence for training-related white matter alterations in brain regions supporting articulation of speech, namely in Broca pars opercularis, left anterior insula, premotor- and primary motor cortex, and in the basal ganglia. Furthermore, since the prefrontal cortex is known to support higher cognitive functions which are strongly engaged during interpreting (Rinne et al., 2000), we hypothesized to find evidence for group differences in the anterior portion of the corpus callosum, a large fibre bundle connecting the two frontal lobes (Nolte, 1999).

In line with our hypothesis, we revealed that language training as experienced by SIs modulates the white matter architecture of brain regions involved in the motor act of speech and supporting sensory-to-motor coupling mechanisms (Bates et al., 2003; Dronkers, 1996; Eickhoff et al., 2009; Mutschler et al., 2007; Wise et al., 1999). These brain regions are the right head of the caudate nucleus and the left anterior insula. Meanwhile, there is evidence showing that the caudate nuclei play a pivotal role in supporting motor aspects of speech by enabling fine-tuned motor adjustments during over language production. This is of particular relevance, for example, for achieving an excellent pronunciation in a foreign language (Abutalebi, 2008; Eickhoff, Heim, Zilles, & Amunts, 2009; Liu, Hu, Guo, & Peng, 2010). Through reciprocal connections with the prefrontal cortex, the basal ganglia not only support motor aspects of speech, but also cognitive functions (Middleton & Strick, 2000; Parent et al., 1995). In fact, there is evidence showing that the basal ganglia are involved in language switching (Abutalebi et al., 2007; Abutalebi, 2008; Crinion et al., 2006; Price et al., 1999) and inhibition functions (Abutalebi et al., 2007; Abutalebi, 2008), the latter being of relevance for example for performing tasks in which one language has to be inhibited for avoiding interferences between the different languages in use. We may speculate whether the altered white matter architecture we revealed in the right head of the caudate nucleus as a function of training may enable a more efficient control of the motor act of speech and of the language in use. Furthermore, the caudate nuclei were previously shown to support language switching and inhibition mechanisms (Crinion et al., 2006; Friederici, 2006).

As a second main result we provide evidence for anatomical differences in the left anterior insula in the SIs in comparison to the control subjects. Previous work conducted with patients (Bates et al., 2003; Dronkers, 1996) as well as with healthy subjects (Ackermann & Riecker, 2004; Riecker, Ackermann, Wildgruber, Dogil, & Grodd, 2000; Wise, Greene, Buchel, & Scott, 1999) clearly demonstrated that this left hemispheric brain region is fundamentally involved in overt speech production and articulation. Furthermore, Golestani and Pallier (Golestani & Pallier, 2007) could show that language expertise, or at least language learning capability, is associated with an altered white mater architecture in the left anterior insula, exactly at the same anatomical location as we revealed in our study. In particular, by performing voxel-based morphometry, the authors revealed that those individuals who more accurately learned to pronounce consonants in a foreign language were characterized by an increased white matter density in a region enclosing the left anterior insula. Other authors have also pointed out that the left anterior insula is engaged in supporting sensory-to-motor coupling mechanisms (Mutschler et al., 2007; Mutschler et al., 2009), which are indeed necessary for performing fast translations at a professional level.

A further main finding of this study was the observation of an altered white matter architecture in the SIs group in the most anterior part of the corpus callosum, a structure which contains fibre bundles connecting the two frontal cortices (Delacoste, Kirkpatrick, & Ross, 1985; Huang et al., 2005; Josse, Seghier, Kherif, & Price, 2008). To date, there is a general consensus that the prefrontal cortex is strongly engaged in supporting higher cognitive functions like attention, memory, inhibition, planning and problem solving mechanisms (Reynolds, McDermott, & Braver, 2006); all

cognitive functions which are necessarily engaged during simultaneous interpreting. The functional contribution of prefrontal brain regions to simultaneous interpreting was previously demonstrated by Rinne and colleagues who performed brain measurements in a group of SIs during interpreting (Rinne et al., 2000). Most interestingly, a previous anatomical study which was dedicated to evaluate the area of five sub-regions of the midsagittal corpus callosum in bilingual and monolingual subjects provided evidence for the fact that anatomical adaptations in the anterior midbody of the corpus callosum probably occur to accommodate multiple language capacities (Coggins et al., 2004). By taking into account this previous evidence, the differential white matter architecture we revealed between the two groups in the anterior portion of the corpus callosum is interpreted as a training-related plastic adaptation which may be useful for increasing the interplay between the two prefrontal cortices during interpreting. In fact, we propose that this morphological difference facilitates the transfer of information across multiple frontal areas, this being advantageous for enhancing executive control. This is in line with previous work conducted with bilingual subjects and highlighting the contribution of extra-linguistic brain functions to the control of multiple languages (Abutalebi et al., 2007; Abutalebi, 2008; Bialystok et al., 2004; Costa et al., 2008; Festman et al., 2010). Certainly, further studies performed with larger samples and different methodological approaches can be useful to better comprehend the contribution of white matter fibre bundles to language expertise.

4.3. Study C

In **Study C** (fMRI) entitled "*Intensive Language Training and Attention Modulate the Involvement of Fronto-Parietal Regions During a Non-Verbal Auditory Discrimination Task"* we investigated functional and behavioural transfer effects originating from intensive language training. With this purpose in mind, we adopted the fMRI technique and measured a group of professional SIs and control subjects while the participants performed a non-verbal discrimination task relying on auditory attention-, and categorization functions. In fact, in order to perform the task subjects have to focus their attention on a particular target stimulus, compare it with the cognitive representation in mind, and to categorize it as the target stimulus by giving a behavioural response. Basing on previous work indicating a strong engagement of attention functions during interpreting (Cowan, 2010), we hypothesized to find a differential engagement of fronto-parietal brain regions as well as an increased number of correct responses in the SIs group in comparison to the controls. This anatomical assumption bases on a plethora of previous work showing the contribution of fronto-parietal brain regions to attention functions across different modalities (Degerman, Rinne, Salmi, Salonen, & Alho, 2006; Johnson & Zatorre, 2006; Pardo, Pardo, Janer, & Raichle, 1990; Rinne et al., 2005; Zatorre, Mondor, & Evans, 1999). Furthermore, basing on previous evidence showing the engagement of left inferior-parietal brain regions during phonetic categorization tasks (Blumstein, Myers, & Rissman, 2005; Joanisse, Zevin, & McCandliss, 2007; Ruff et al., 1981; Turkeltaub & Coslett, 2010), we assumed that individuals trained to perform fast phonological distinctions with minimal errors may have developed a more efficient neural system for categorizing acoustic cues. In line with our hypothesis, we revealed a differential engagement of frontal and parietal brain regions, which was associated

with the attentive discrimination of the target stimuli and independent from the brain responses induced by the acoustic perception per se, between the two groups. Surprisingly, these differential brain responses we revealed between the two groups were not accompanied by behavioural differences.

Certainly, simultaneous interpreting can be considered as an extremely complex language task which not only requires exceptional language skills in more than one language, but most notably also the engagement of executive control function like attention, working memory, inhibition, and language switching mechanisms (Abutalebi et al., 2007; Christoffels et al., 2006; Cowan, 2010; Daro et al., 1994; Rinne et al., 2000). Even though to date there is evidence for different attentional sub-systems operating hand in hand with a variety of perceptual and cognitive control functions (Mirsky, Anthony, Duncan, Ahearn, & Kellam, 2010; Posner & Boies, 1971), the engagement of frontal and parietal brain regions during attention tasks was consistently reported across a variety of sensory modalities (Degerman et al., 2006; Johnson et al., 2006; Pardo et al., 1990; Rinne et al., 2005; Zatorre et al., 1999). Notably, our results not only indicated a differential functioning of fronto-parietal brain regions in language experts while performing a non-verbal attention task, but also point to a systematic reorganization of auditory-related top-down functions. In particular, we observed a functional displacement of attention functions from frontal to parietal brain regions, which was reflected by reduced brain responses in the right frontal lobe and as well as by increased brain activity in the left inferior parietal lobe. We may speculate whether this displacement of attention functions from anterior to posterior brain regions may be advantageous for releasing the frontal cortex, which is indeed strongly involved in simultaneous interpreting, from additional cognitive loads.

This line of argumentation is supported by previous work showing a strong functional engagement of prefrontal brain regions during simultaneous interpreting (Rinne et al., 2000) as well as during multilingual speech processing (Abutalebi et al., 2007).

An alternative perspective which may be useful for explaining the differential brain responses we revealed between the two groups in frontal and parietal brain regions without involving attention as the domain of cognition affected, is that the intensive language training experienced by SIs may be associated with a functional specialization of the parietal "categorization system". This implies that persons specifically trained to convert an input language to an adequate output format may rely to a lesser extent on frontal control mechanisms while performing top-down decisions about the nature of auditory presented features. This is plausible, than the left inferior parietal lobe was previously shown to be involved in phonetic categorization functions (Blumstein et al., 2005; Joanisse et al., 2007; Ruff, Marie, Celsis, Cardebat, & Demonet, 2003; Turkeltaub et al., 2010). For example, Blumstein and co-workers (Blumstein et al., 2005) presented to the subjects a voice onset continuum of syllables during a phonetic categorization task and revealed that a particular brain region situated in the left inferior parietal lobe, namely the angular gyrus, was particularly responsive to the "best fit" to a phonetic category. This previous result is in line with our observations and may imply that professional language training as experienced by SIs favours the categorization of acoustic information.

5. GENERAL DISCUSSION

In this section I will discuss the results of the three studies implemented in this Ph.D. thesis by putting them in a broader context. A common denominator of the three studies is that I provide evidence for the fact that neuroplasticity primarily arises in brain regions supporting cognitive control mechanisms and articulation rather than in those involved in linguistic functions per se. This observation is in agreement with previous work conducted with bilingual subjects (Abutalebi et al., 2007; Abutalebi, 2008) and evidences that multilingual speech competence constitutes more than only language representation per se. Since the specific results of the three studies included in this Ph.D. thesis have already been extensively discussed in the original publications, in this section I will focus on the contribution of extra-linguistic brain functions to language expertise only.

The present Ph.D. thesis aimed at contributing to the ongoing debate on functional and structural neuroplasticity as well as transfer effects originating from intensive language training and expertise. Basing on a vast amount of research performed with bilingual and multilingual subjects, meanwhile there is a convergence of results indicating that later-acquired languages overlap with the cortical representation of the first language, the degree of overlapping depending from variables like age of acquisition and proficiency (Perani et al., 1998; Perani et al., 2005). Otherwise, there is also convincing evidence pointing to fact that the control of L2 languages necessitates increased neuronal resources and computational demands in comparison to L1 languages (Abutalebi et al., 2007; Perani et al., 2005). Exactly these increased computational demands which are necessary for controlling multiple languages were previously extensively described by Abutalebi and co-workers

(Abutalebi et al., 2007), as well as by Rodriguez-Fornells and colleagues (Rodriguez-Fornells, Balaguer, & Munte, 2006), and proposed to be dependent on the contribution of extra-linguistic brain functions. This framework bases on the assumption that multilingual speech competence not only depends on an adequate representation of linguistic information in the brain, but most notably also on the engagement of cognitive processes which are necessary for controlling multiple languages at the same time. In this context, Abutalebi and Green (Abutalebi et al., 2007) described at least four neuronal devices which are assumed to be responsible for administrating multiple levels of cognitive control in multilingual subjects, namely the prefrontal cortex, the anterior cingulate, the basal ganglia, and the inferior parietal lobe. Whereas each of these systems is presumed to be engaged in specific aspects of cognition like working memory, inhibition, attention, or language switching, cognitive control emerges from the integration of all these systems. Meanwhile, there is also evidence pointing to a relationship between multilingual speech competence and plastic alterations in brain regions supporting articulation of speech (Golestani et al., 2007) and sensory-to-motor coupling mechanisms (Simmonds, Wise, Dhanjal, & Leech, 2011). These plastic alterations are presumed to be necessary for enabling an optimal tuning of the speech output while formulating in a target language, for learning foreign speech sounds, as well as for comparing the speech input with its respective translation.

The engagement of extra-linguistic brain functions during multilingual speech processing becomes particularly evident by considering that cognitive and motor control is needed for example for producing sounds in the weaker language (Abutalebi et al., 2007; Hernandez, Martinez, & Kohnert, 2000), switching between

languages (Garbin et al., 2011), performing translation and interpreting tasks (Christoffels et al., 2006; Price, Green, & von Studnitz, 1999; Rinne et al., 2005), as well as for accomplishing language tasks in which one language has to be actively inhibited (Rodriguez-Fornells, Rotte, Heinze, Nosselt, & Munte, 2002). Notably, the strong demands placed on the cognitive functions of multilingual subjects are also reflected by several behavioural studies showing for example increased attention (Bialystok et al., 2004; Costa et al., 2008) and inhibition (Bialystok et al., 2004; Festman et al., 2010) functions in bilingual subjects, in comparison to monolinguals, even in domains which were not explicitly trained. Meanwhile there is also some behavioural (Christoffels et al., 2006; Daro et al., 1994) and neuroimaging (Hervais-Adelman et al., 2011; Price et al., 1999; Rinne et al., 2000) evidence showing that the framework proposed by Abutalebi and Green (Abutalebi et al., 2007) and primarily describing the neurocognition of language representation and control in bilingual subjects, is valid for language expertise as experienced by SIs as well.

In the present work I propose that the investigation of SIs may be a fruitful alternative approach for better comprehending how multiple languages are represented and controlled in the brain. In fact, it is reasonable to think that a particular set of brain regions and functions are particularly devoted to sustain cognitive control during multilingual speech processing, the degree of engagement of these brain regions probably depending on the task demands, the proficiency achieved, and on the degree of expertise and training. In line with this, and by considering that simultaneous interpreting constitutes a very complicated language task that engages cognitive and motor control functions even more than in bilingual subjects, the investigation of SIs can contribute to better understand how multiple languages are

controlled in the brain. The strong engagement of cognitive and motor control functions during interpreting becomes particularly evident by considering that SIs handle several operations at the same time. This implies that SIs have to perceive and decode the source language, keep the input language in working memory while converting the meaning to the target language, switch between languages, formulate in the target language while inhibiting the motor output of the input language, as well as attentively monitor both the input and the output channels.

In conclusion, the results reported in this Ph.D. thesis are in line with the seminal framework proposed by Abutalebi and Green (Abutalebi et al., 2007) and point to a massive influence of professional language training on the functional and structural architecture of brain regions involved in controlling multiple levels of cognition and articulation, rather than on linguistic representation per se. I want to emphasize that even though to date an impressive number of work has summarized the enormous progress which has been done for understanding how multiple languages are represented and controlled in the brain, the exact functioning of the neuronal devices responsible for administrating cognitive control remains to be fully described (Hervais-Adelman et al., 2011). Hopefully, due to the strong processing demands associated with simultaneous interpreting, future studies performed with SIs will enable to better understand the mechanisms underlying the control of multiple languages and transfer effects.

6. ABBREVIATIONS

AG: Angular Gyrus

aIFG: Anterior Inferior Frontal Gyrus

ATC: Anterior Temporal Cortex

BA: Brodmann Area

BOLD: Blood Oxygen Level-Dependent

DNA: Deoxyribonucleic Acid

DTI: Diffusion Tensor Imaging

EE: English-English

EEG: Electroencephalography

EG: English-German

ERD: Event-Related Desynchronisation

ERP: Event-Related Potential

ERS: Event-Related Synchronisation

fMRI: Functional Magnetic Resonance Imaging

GE: German-English

GG: German-German

IFG: Inferior Frontal Gyrus

FA: Fractional Anisotropy

L1: Native Language

L2: Non-Native language

LH: Left Hemisphere

LTD: Long Term Depression

LTP: Long Term Potentiation

MEG: Magnetoencephalography

MR: Magnetic Resonance

MRI: Magnetic Resonance Imaging

mRNA: Messenger Ribonucleic Acid

ms: Milliseconds

MTG: Middle Temporal Gyrus

N400: Electrophysiological Response

PET: Positron Emission Tomography

Ph.D.: Doctor of Philosophy

pIFG: Posterior Inferior Frontal Gyrus

PT: Planum Temporale

RH: Right Hemisphere

SIs: Simultaneous Interpreters

VBM: Voxel-Based Morphometry

7. CURRICULUM VITAE

Name:	Stefan Elmer
Personal:	Born 01.08.1978 in Sorengo, Switzerland
Address:	University of Zurich Institute of Psychology Division Neuropsychology Binzmühlestrasse 14/25 CH-8050 Zürich Switzerland
Email	s.elmer@psychologie.uzh.ch
Phone	+41 44 635 73 98

Academic Education and Qualifications:

01.03.2010 - current	Postdoctoral researcher Division Neuropsychology, Institute of Psychology, University of Zurich, Switzerland
01.03.2010	Ph.D. in Neuropsychology Division Neuropsychology, Institute of Psychology, University of Zurich, Switzerland
	Ph.D. Thesis: “Functional and anatomical correlates of language expertise” (summa cum laude)
	Supervisors: Lutz Jäncke, Prof. Dr.; Martin Meyer, Prof. Dr.

Since 2006	Assistant / Ph.D. student Division Neuropsychology, Institute of Psychology, University of Zurich, Switzerland Supervisors: Lutz Jäncke, Prof. Dr.; Martin Meyer, Prof. Dr.
2006	Master of Science (M.Sc.) in Psychology, Neuropsychology, and Psychopathology. Institute of Psychology, University of Zurich, Switzerland Master Thesis: “Die Vorstellung von verbalen und musikalischen Stimuli in der auditorischen Modalität: eine LORETA basierte AEP/EEG Studie”, Supervisors: Lutz Jäncke, Prof. Dr.; Martin Meyer, Prof. Dr.
2002	Master of Science (M.Sc.), Turn- und Sportlehrer Studium ETH Zurich, Switzerland Master Thesis: "Der Einfluss der Aussentemperatur auf die mechanische Leistung im anaeroben Bereich: Messreihen am Fahrradergometer“ Supervisor: Dr. Jachen Denoth

Research and Clinical Experience:

Since 01.03.2010	Postdoctoral researcher Division Neuropsychology, Institute of Psychology, University of Zurich, Switzerland
Since 2006	Research Fellow Division Neuropsychology, Institute of Psychology, University of Zurich, Switzerland Supervisors: Lutz Jäncke, Prof. Dr.; Martin Meyer, Dr.
2004	Student Research Fellow (Tutorat) Division Neuropsychology, Institute of Psychology, University of Zurich, Switzerland Supervisor: Martin Meyer, Prof. Dr.
01.10 - 31.12 2004	Internship “Psychopathologie des Erwachsenenalters” psychiatrische Klinik Beverin (GR), Switzerland Supervisor: Dr. Reto Parpan
01.03 - 31.4 2003	Internship “Psychopathologie des Erwachsenenalters” Organizzazione Sociopsichiatrica Mendrisio (TI), Switzerland Supervisor: Dr. Chiara Ferrazzo

Teaching Experience:

2012	Seminar "Neuropsychological Therapies" Division Neuropsychology, Institute of Psychology, University of Zurich, Switzerland
2009	Workshop “Neuroscience and Plasticity” Hochschule für Heilpädagogik (HfH) Zurich, Switzerland
2009	Workshop "EEG measurements and data evaluation" Division Neuropsychology, Institute of Psychology, University of Zurich, Switzerland
2008	Workshop "EEG measurements and data evaluation" Division Neuropsychology, Institute of Psychology, University of Zurich, Switzerland

Fellowships and Awards:

2010	Travel grant from the Zentrum für Neurowissenschaften Zürich (ZNZ) for the participation at the Organization for Human Brain Mapping’s annual meeting in Barcelona (Spain)
2009	Travel grant from the Zentrum für Neurowissenschaften Zürich (ZNZ) for the participation at the Organization for Human Brain Mapping’s annual meeting in San Francisco (U.S.A)

Member of Scientific Associations:

OHBM	Organization for Human Brain Mapping
ZNZ	Neuroscience Center Zurich

Peer - Reviewed Publications:

Elmer, S., Rogenmoser, L., Meyer, M., and Jäncke, L. (2012). Pre-attentive binding of tones and colours in the auditory cortex of synaesthetes. Under review.

Elmer, S., Hänggi, J., Meyer, M., and Jäncke, L. (2012). Increased cortical surface area of the left planum temporale favours the discrimination of temporal speech information in musicians. Under review.

Elmer, S. (2012). The investigation of simultaneous interpreters as an alternative approach to address the signature of multilingual speech processing. Under review.

Kühnis, J., Elmer, S., Meyer, M., and Jäncke, L. (2012). Musicianship boosts perceptual learning of pseudoword-chimeras: an electrophysiological approach. Under review.

Meyer, M., Elmer, S., and Jäncke, L. (2012). Musical expertise induces neuroplasticity of the planum temporale. Accepted for publication. Ann NY Acad Sci.

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Elmer, S., Burkard, M., Renz, B., Meyer, M., and Jancke, L. (2009). Direct current induced short-term modulation of the left dorsolateral prefrontal cortex while learning auditory presented nouns. Behav. Brain. Funct. doi: 10.1186/1744- 9081-5-29.

Meyer, M., Elmer, S., Baumann, S., and Jancke, L. (2007). Short-term plasticity in the auditory system: differential neural responses to perception and imagery of speech and music. Restor. Neurol. Neurosci. 25:411-431.

Published Abstracts and Conference Posters:

2011 Human Brain Mapping, Quebec (Canada)
Functional and anatomical correlates of phonetic and temporal categorization in professional musicians.
Elmer, S., Hänggi, J., Meyer, M., and Jäncke, L.

2010 Human Brain Mapping, Barcelona (Spain)
Anatomical correlates of language expertise.
Elmer, S., Hänggi, J., Meyer, M., and Jäncke, L.

2009 Human Brain Mapping, San Francisco (USA)
Simultaneous interpreters as a model for neuronal adaptation in the domain of language processing.
Elmer, S., Meyer, M., and Jäncke, L.

2009 Zentrum für Neurowissenschaften, Zurich (Switzerland)
Direct current-induced short-term modulation of the left dorsolateral prefrontal cortex while learning auditory presented nouns.
Elmer, S., Burkard, M., Renz, B., Meyer, M., and Jäncke, L.

2008 Zentrum für Neurowissenschaften, Zurich (Switzerland)
ERP differences of prelexical processing between dyslexic and non-dyslexic children.
Kast, M., Elmer, S., Jäncke, L., and Meyer, M.

2007	Zentrum für Neurowissenschaften, Zurich (Switzerland) Short-term plasticity in the auditory system: differential neural responses to perception and imagery of speech and music. Elmer, S., Meyer, M., and Jancke, L.

Invited Talks:

10.05.2011	Zürcher Kompetenzzentrum Linguistik, University of Zurich, Switzerland Auf der Spur der Evolution der Sprache: eine biologische Perspektive.
03.03.2011	Linguistisches Forschungskolloquium University of Zurich, Switzerland Wie das Gehirn den Umgang mit Mehrsprachigkeit bewältigt und Sprachexpertise ermöglicht.
23.10.2010	Swiss Athletics, Centro sportivo Tenero, Switzerland La preparazione mentale nello sport dalla prospettiva della neurobiologia.
15.05.2010	Swiss Athletics, Haus des Sportes, Ittigen, Switzerland Mentales Training und Gehirn. Forum "Mythos mentale Fähigkeiten im Sport"

12.01-14.01 2009	Hochschule für Heilpädagogik (HfH), Zurich, Switzerland
19.01-21.01.2009	Workshop
	Der Einfluss der Umwelt auf die neuronale Entwicklung.

Ad Hoc Reviewer	European Journal of Neuroscience
	Plos One
	Journal of Neurolinguistics
	Frontiers in Auditory Cognitive Neuroscience
	Zeitschrift für Neuropsychologie
	Neuroreport
	BMC Neuroscience
	Neuroimage

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